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Effet de la diversité végétale sur la production des systèmes de culture multi-espèces, cas des systèmes agroforestiers de Talamanca, Costa Rica

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Avant-propos

Depuis les débuts de l'agriculture, les humains ont simplifiés la composition végétale des parcelles cultivées. Cette simplification s'est encore renforcée au XX^{ème} siècle avec l'avènement de la mécanisation et de l'utilisation des produits phytosanitaires. Le principe que les mélanges d'espèces doivent amener une meilleure production n'est pas nouveau. Déjà en 1859, Charles Darwin suggérait: "It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised." (On the origins of species, first British edition (1859), page 113). Actuellement, de nombreuses études d'écologie sur les systèmes naturels ont montrées que dans de nombreuses conditions, un plus grand nombre d'espèces amène à une plus grande productivité, une meilleure stabilité de cette productivité, et une amélioration de la résilience aux perturbations naturelles. Cependant, l'influence de la diversité spécifique sur la production agronomique est moins évidente et pas toujours vérifiée. Aujourd'hui la diversification végétale des agrosystèmes est souvent présentée comme une perspective prometteuse, même si les systèmes complexes qui en résultent sont forcément plus difficiles à gérer au niveau agronomique. Il est donc opportun de mieux caractériser les règles qui lient la diversité végétale et les performances agronomiques.

La recherche étudie de plus en plus les systèmes agroforestiers tropicaux comme un modèle alternatif à l'agriculture intensive. Les chercheurs ont décrits comment ces systèmes participent à la conservation de la biodiversité et à la fourniture de services écosystémiques. Dans la perspective de mieux gérer ces systèmes, il est devenu important de démêler les interactions entre la diversité végétale (incluant ses organisations horizontales et verticales) avec les processus de l'écosystème (partage des ressources lumineuse et en nutriments, recyclage des éléments…). Aborder ces questions dans le cas des systèmes agroforestiers tropicaux est clairement une tâche difficile, mais cela représente aussi un cas extrême qui devrait être utile pour mieux comprendre les autres systèmes plus simples.

En tant que chercheur à l'Institut technologique du Costa Rica (Tecnológico de Costa Rica, TEC) depuis 2010, j'ai mené des recherches dans la région de Talamanca dans la province de Limón (sud-est du Costa Rica) avec l'objectif de combiner les savoirs indigènes ancestraux avec des techniques agronomiques innovantes afin de tenter d'améliorer la production de ces systèmes agroforestiers. Cette activité a souvent été limitée par le niveau d'éducation assez bas des populations, le manque d'infrastructures et le niveau de développement global de la région. Le sujet de la thèse présenté ici est une suite logique qui devait me permettre de disposer d'éléments quantifiés sur le rôle de la composition spécifique de ces systèmes sur leur production, mais aussi de mieux comprendre leurs limites. Le travail expérimental de cette thèse a été possible grâce à l'aide et l'intérêt des agriculteurs de la région de Talamanca. J'ai mené ce travail depuis décembre 2015 jusqu'à septembre 2017. La partie expérimentale a été réalisée dans la région de Talamanca entre mars 2015 et mai 2016, ensuite de juin 2016 à septembre 2017, j'ai travaillé à Montpellier au sein de l'équipe GECO du CIRAD.

Dans ma thèse, le focus a été fait sur la quantification de la relation diversité/productivité dans le cas des systèmes agroforestiers de Talamanca ; avec à la fois de implications 'fondamentales' et appliquées. Cela m'a permis d'établir des règles générales liant la diversité des plantes cultivées (et leur organisation spatiale) avec la productivité de ces systèmes de manière globale, mais aussi avec celle de deux cultures clés de ces systèmes : les bananiers et les cacaoyers. Il a été particulièrement intéressant d'examiner mes résultats à la lumière de grandes questions d'écologie, comme par exemple la « gradient stress hypothesis » qui suppose que la relation entre la diversité végétale et la productivité est positivement affectée par la compétition pour les ressources. D'un point de vu appliqué, mon travail a été l'opportunité de quantifier la production globale de ces systèmes et de comprendre jusqu'où la diversité fonctionnelle peut la modifier. Cela a été particulièrement stimulant d'interpréter ces résultats à la fois avec le regard de l'agronome et celui de l'écologue. L'originalité de mon approche a été de mobiliser une approche individu-centrée pour tenter de comprendre comment l'organisation spatiale pouvait modifier la production des deux principales cultures de rente (bananiers et cacaoyers). Cette

approche a permis de déterminer comment l'abondance des voisins d'une plante donnée dans un rayon donné influence son rendement. De manière complémentaire, j'ai mené une méta-analyse qui visait à étudier la relation diversité végétale-productivité dans un grand nombre de conditions et de mieux comprendre le rôle de facteurs tels que la latitude, le type de plante considéré ou la structure verticale de la canopée. Il a été particulièrement riche d'analyser les résultats de cette méta-analyse et de la partie expérimentale en mobilisant les mêmes concepts.

Ce travail a donné lieu à trois publications (chapitre 3, 4, 5), ainsi qu'à cinq présentations lors de congrès (3 communications orales et 2 posters) :

Articles soumis, en révision

- **Salazar-Diaz, R.** & Tixier, P., 2016. Effect of plant diversity on income generated by agroforestry systems in Talamanca, Costa Rica. Agroforestry System Journal

- **Salazar-Diaz, R.** & Tixier, P., 2017. Responses of productivity to plant richness: A meta-analysis relevant to the diversification of agricultural ecosystems. Agronomy for Sustainable Development

- **Salazar-Diaz, R.** & Tixier, P., 2017. Individual-based analysis of interactions between plants: a statistical modelling approach applied to banana and cacao in heterogeneous multistrata agroecosystems. European Journal of Agronomy

Communications orales

- **Salazar-Diaz, R.** & Tixier, P., 2016. *Effect of plant diversity on the global productivity of agroforestry systems in Talamanca Costa Rica***.** 3rd European Agroforestry Conference. 23-25 May 2016, Montpellier France.

- **Salazar-Diaz, R.** & Tixier, P., 2016. *Productivity of agroforestry systems in Talamanca, Costa Rica*. WCF/USDA Cocoa Borlaug Fellowship Program. 20-24 Feb 2017, Guayaquil, Ecuador.

- **Salazar-Diaz, R.** & Tixier, P., 2016. *Effect of plant diversity on the production of multi-species cropping systems, case of agroforestry systems in Talamanca*. Réunion PITTA-CACAO, Ministère de l'Agriculture de Costa Rica. 26 Aug 2017, San Jose, Costa Rica.

Posters

- **Salazar-Diaz, R.** & Tixier, P., 2016. *Effect of multi-species cropping system on agricultural performance in Talamanca Costa Rica.* 5th International EcoSummit, 29 Aug-1 Sep 2016, Montpellier, France.

- **Salazar-Diaz, R.** & Tixier, P., 2016. *Effect of plant diversity on the global productivity of agroforestry systems in Talamanca Costa Rica***.** 3emes Journées des Doctorants de l'M2E, 22-23 Mars 2017, Montpellier, France.

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Chapter 1 – General Introduction

1. Understanding the heterogeneity of plant association and productivity

1.1 General relation between diversity and productivity

The agricultural revolution of the 20th century is associated with intensification and simplification of agricultural practices with the aim to increase yield which was in detriment of biodiversity, affecting both wild species whose habitat disappears and cultivated species whose genetic diversity was often greatly reduce. The expansion and intensification of agricultural activities are causing the progressive fragmentation of forest habitats and a significant loss of biodiversity (Tilman et al. 2002). The impact on the environment of the massive use of fertilizers, phytosanitary products and fossil energies to attend the mechanization of works of these simple agricultural systems, is now well known and documented (Eddleston et al. 2002, Aubertot et al. 2005).

Biodiversity in agricultural systems is now a major concern and promises to be a major issue of the 21st century (Plantureux et al. 2005) Biodiversity was often presented as increasing the efficient use of resources and promoting positive interaction between species and other ecosystem processes (Tilman and Pacala 1993, Hooper et al. 2005, Nakamura 2008, Smith et al. 2008, Cardinale et al. 2012b). The effect of plant diversity on productivity has long been studied in natural systems (Naeem et al. 1994, Loreau et al. 2001). But in agricultural systems there is still debate about how plant diversity can be increased without decreasing productivity and making management too difficult for farmers (Swift et al. 2004). According to Lehman and Tilman (2000), diversity increases community productivity but may reduce the productivity of individual species.

There is thus a need to understand the type of plant to be used for the diversification of agricultural ecosystems and the optimal degree of diversification, regarding the exact role of biodiversity in ecosystem functioning

and the approaches that should be adopted to enhance crop productivity (Huston 1997, Tilman 1997, Loreau et al. 2001, Aarssen et al. 2003).

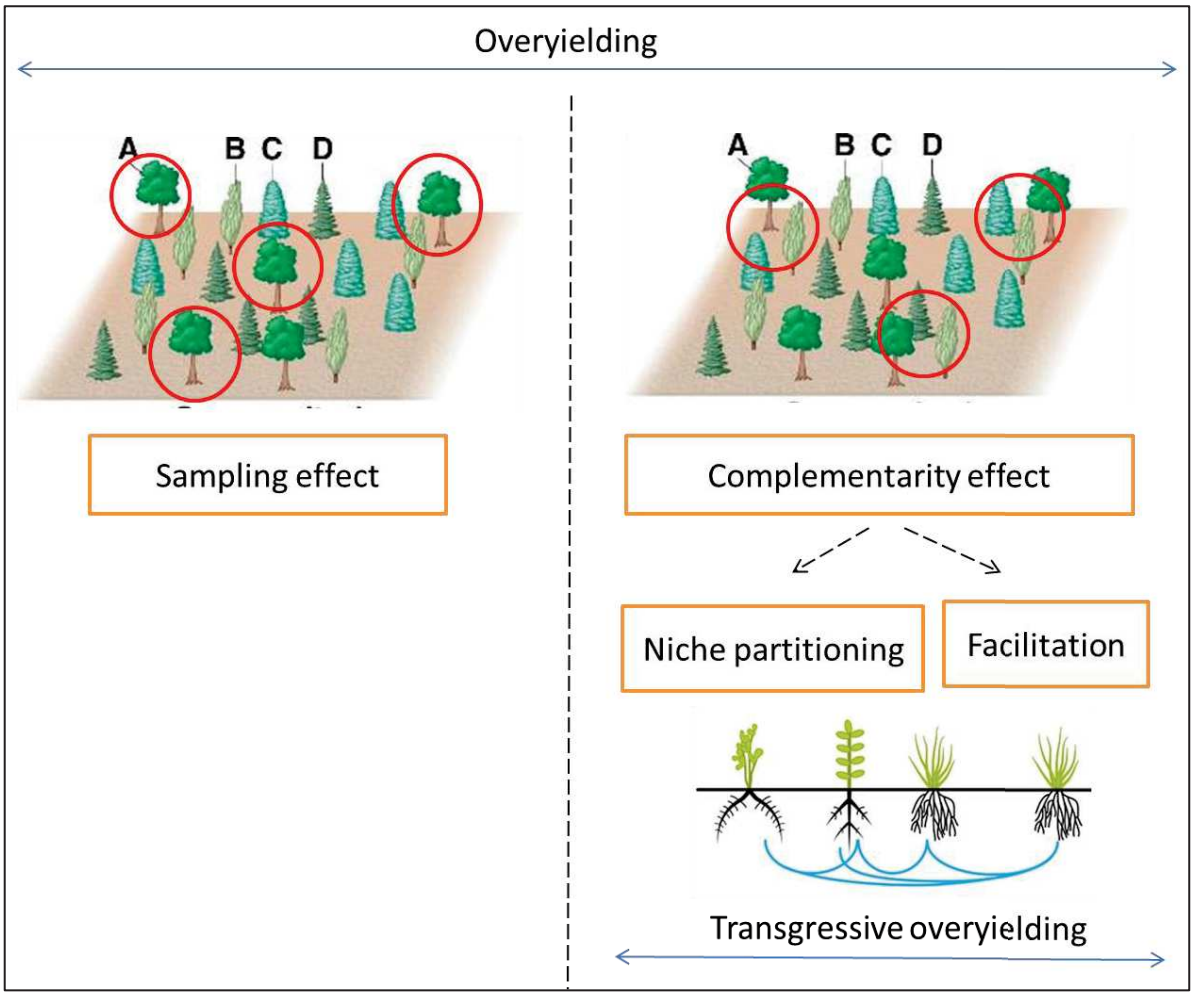

Figure 1. *General arguments over two types of mechanisms invoked to explain how and why a mixture of species outperforms monocultures: Sampling effect and complementarity. Sampling effect occur when the most productive species come to dominate the biomass of species rich polyculture. Complementarity hypothesis propose that species rich plantation are able to more efficiently access and utilize limiting resources because they contain species with diverse array ecological attributes. Generally, the complementarity effect includes both niche differentiation and facilitation; in practice, it is usually difficult to distinguish them. Complementarity effects may increase total ecosystem production, sometimes leading to a production higher than that of the most productive monoculture. This is called transgressive overyielding.*

1.2 Mechanisms influencing biodiversity-productivity relationship

The net effect of biodiversity enhancing productivity in agricultural ecosystems has been traditionally explained by potentially important types of mechanisms such complementarity and sampling effects (Hector et al. 1999, Yachi and Loreau 2007) (see **Figure 1**). Sampling effect occur when the most productive species come to dominate the biomass of species rich polyculture, and the probability to have very productive species increase (which should also be strong competitive and should dominate the community) when the number of species of the community increases (Cardinale et al. 2007), but the most common assumption is complementarity hypothesis, that propose that species rich plantation are able to more efficiently access and utilize limiting resources because they contain species with diverse array ecological attributes (Kelty 1992, Tilman 1999). Generally, the complementarity effect include both niche differentiation (differential resource utilization for coexistence of species) and facilitation (positive interactions between organisms that benefit at least one of the participants and cause harm to neither), because distinguish between them is difficult in practice (Loreau and Hector 2001, Bruno et al. 2003, Begon et al. 2006).

There are differences between agronomists and ecologists in addressing the development of more sustainable production systems (see **Figure 2**). Ecologists usually focus on understanding the mechanisms of species coexistence (Kneitel and Chase 2004, Roxburgh et al. 2004) and agronomists focus on management strategies to increase and stabilize yield (Malézieux 2012). To favor this development, there are considerable interests to unify these points of view and methods to better understand the competition / complementarity processes in diversified plant communities and not only address coexistence questions (Bruno et al. 2003, Malézieux 2012, Barot et al. 2017). It is of major importance to quantify the tight balance between negative effects of competition (which can lead to lower productivity of some species) and complementarity and facilitation effects (which can enable greater productivity at the community level).

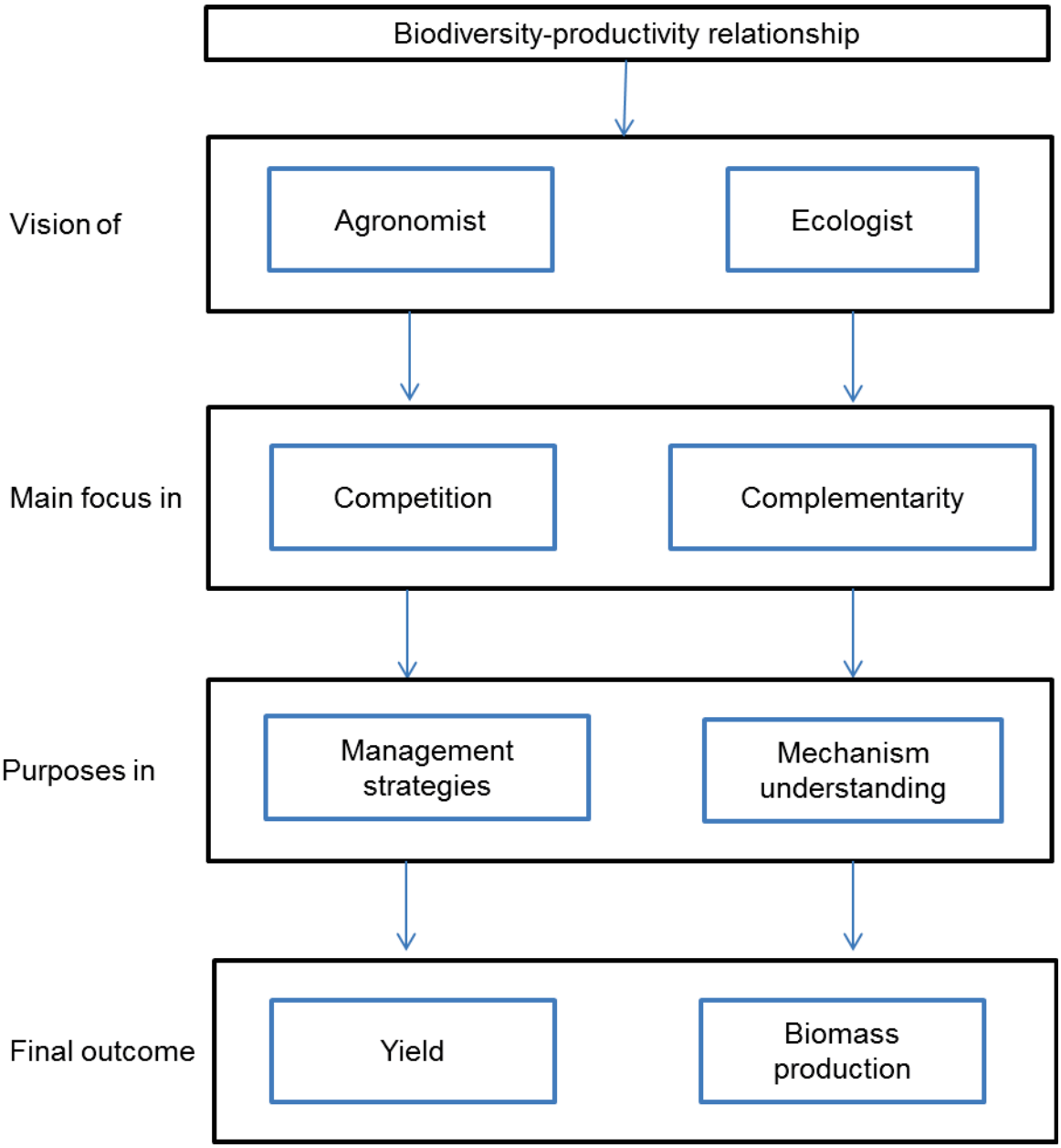

Figure 2. *Passage of certain differences across the emphases in the agronomist and ecologist areas on the biodiversity-productivity relationship, (top row), distinction between main focus mechanisms across areas (second row), differences between the main purposes (third row), and finally the outcome expected.*

Effects of environmental factors on ecosystem productivity

Fridley (2002) suggested that environmental factors should have a much stronger effect on local ecosystem functions (including productivity) than the diversity of the species pool, for example local environmental may or may not promotes resource partitioning and facilitation processes. Cardinale, Nelson & Palmer (2000) argued that the diversity-productivity relationship changes with environmental context and that the form and causes of this relationship may be highly dynamic over time and space.

In productive ecosystems with high plant biomass, competitive exclusion by a small number of highly competitive species is hypothesized to constrain species richness (Grime 1998). According to Mulder et al. (2001), environmental stress favors a positive relationship between plant species richness and productivity because such stress limits the importance of competition. However, Maestre et al. (2005) rejected the stress-gradient hypothesis (which states that stress enhances facilitation between neighbors) and concluded that neither positive nor negative effects of neighbors increased with abiotic stress because species interactions across abiotic stress gradients do not follow a simple pattern. To date, there is a lack of general knowledge on the conditions in which overyielding is likely or not likely to occur.

1.3 Role of spatial organization

Even in a local environmental context and in a field composed of plants of the same species, the processes that determine how individual plants compete for resources are complex. (Sinoquet and Cruz 1995). The spatial organization of individuals in a community may be one of the most important structural characteristics that influence complementarity between species, biodiversity, and ecosystem functioning (Mokany et al. 2008, Perfecto and Vandermeer 2008, Pringle et al. 2010). To our knowledge, there is a lack of tools able to disentangle the effect of spatial organization of the plant community on plant performances, especially in complex systems.

Cardinale, Nelson & Palmer (2000) showed that the amount of variation in productivity explained by species diversity increased with spatial heterogeneity.

Grime (1998) suggested that the relationship between diversity and ecosystem properties could be usefully investigated by classifying species according to their architecture. However, few authors have tried to link the structural complexity of different land uses to productivity, but see (Steffan-Dewenter et al. 2007). Understanding how the spatial organization of plants affects productivity is important for improving the design and management of complex systems (Baskent and Jordan 1996). However, the substantial spatial heterogeneity of highly diversified systems makes this task challenging. In such complex systems, each plant has a unique “neighborhood”, making the establishment of generic rules at the field scale extremely difficult.

Although spatial heterogeneity of plants is recognized as a powerful promoter of coexistence between plants (Monzeglio and Stoll 2005), explaining species performances remains challenging in fields where the main characteristics of multispecies communities is the wide range of spatial (vertical and horizontal) structure of species mixture (Bhagwat et al. 2008, Malézieux et al. 2009, Lamanda et al. 2012).

Complex multispecies system can include a high associated plant species; there is thus a need for farmers to understand the optimal degree of diversification that should be adopted to enhance crop productivity, reason why spatial organization is an important factor to study because farmers can manage it and it is a way to optimize the system.

1.4 An agroecology approach to improve production

Intensive agriculture, which attempts to maximize yield under favorable abiotic and biotic conditions allowed by the large use of chemical inputs and mechanization, has led to an important reduction in plant diversity and had important detrimental environmental impacts (Tilman et al. 2002). There is now increasing interest in developing agricultural systems that i) limit the use of chemical inputs and fuel, ii) tolerate unpredictable climate and biotic stresses (Lane and Jarvis 2007, Varshney et al. 2011), iii) maintain acceptable yields. The complementarity between plants of diverse species or genotypes may be a useful way to improve crop production and its stability (Vandermeer 1992, Isbell et al.

2015a). The diversification of agricultural systems can be achieved through a variety of options, according to a gradient of complexity, including the number and type of plant species, the horizontal and vertical structure of the mixture, and the life cycle duration of the species, for example: row intercropping, mixed intercropping, row agroforestry, complex agroforestry (Altieri 2002, Malézieux et al. 2009).

Study, which factors affect the relationship between diversity and productivity? is an important step to better understand how agroecology may be used to improve production.

1.5 Case of tropical agroforestry

Agroforestry is an example of such diverse system. It is expected that in tropical agroforestry systems where semi-perennial and perennial crops are associated with trees, productivity will be enhanced by diversity, since biodiversity increase the range of services that these agroecosystems provide (Nair 1993) with the aim of improving social, economic and environmental benefits (Torquebiau 2007).

Researchers are increasingly studying tropical agroforests as models for sustainable agricultural systems, proposed as a sustainable alternative to modern intensive agricultural systems; conserving biodiversity and ecosystem services, while providing significant local livelihood (Sperber et al. 2004, Leakey et al. 2005, Tscharntke et al. 2011, Ngo Bieng et al. 2013).

Tropical agroforests are characterized by associations of multi-strata, multi-functional, and uneven-aged trees and crops, resulting in high species richness and complexity of spatial structure (Sanchez 1995, Ngo Bieng et al. 2013). The importance of agroforestry systems in providing ecosystem services (such as carbon sequestration and biodiversity conservation) has been documented, but have paid far less attention to how the overall productivity of such agroforests is related to their structure (Somarriba and Harvey 2003, Suatunce et al. 2003).

Many people in developing tropical countries depend on agroforestry systems for subsistence, economic income, and other services (Malézieux et al. 2009, Cerda et al. 2014, Paul et al. 2015). In addition to generating timber and firewood as a long-term income, agroforestry can also provide supplementary income from

associated perennial and semi-perennial crops as a short-term income (Nair 2007). In many systems, however, the efficiency of agroforestry farms have not been determined, i.e., there is still a need to quantify the costs and benefits of agroforestry farms in order to justify their propagation and adoption (Molua 2003). From both private and social perspectives, the economic potential of agroforestry farms still need to be well studied (Franzel and Scherr 2002, Molua 2003, Rasul and Thapa 2006). The combined productivity and profitability of all cultivated plants in the system, have scarcely been addressed in complex agroforestry systems.

2. Scientific questions

The central objective of my thesis is to **understand how plant diversity (mainly functional diversity), its spatial organization, and its management, alter the yield of cacao-banana agroforestry systems in the region of Talamanca, Costa Rica**. Understanding the link between biodiversity and productivity is pivotal in the context of the diversification of agricultural systems. On a methodological point of view, it is necessary to develop tools able to tackle the diversity-productivity issue in multi-strata systems under the management of farmers. To our knowledge, sufficient measurements to build such tools have only been obtained in relatively homogeneous multi-strata systems as coffee agroforestry systems that are less diverse and complex than cacao-banana agroforestry systems (Roupsard et al. 2011, Charbonnier et al. 2013).

Few quantitative syntheses regarding the relationship between diversity and productivity have included a wide range of species in different ecosystems with different environmental gradients from both agricultural and natural systems. To help to establishing global trends, it is important to comparison standardized measures of the effect of plant diversity on system productivity across a wide range of conditions (latitudes, climates, number of canopy strata, and types of plants) in both agricultural and natural ecosystems. In agricultural systems, the debate is still about how plant diversity can be increased without decreasing

productivity. There is thus a need to understand i) the type of plant to be used for the diversification of agricultural ecosystems, ii) the optimal degree of diversification, and iii) in which conditions biodiversification is more likely to be an efficient option. My first scientific question is thus:

Question 1

Which factors affect the relationship between plant diversity and productivity?

Traditional agroforestry systems have been suggested to be a promising land use strategy, conserving a significant proportion of tropical rain forest diversity while providing significant economic returns (Steffan-Dewenter et al. 2007, Perfecto and Vandermeer 2008). The biodiversity benefits of traditional tropical agroforestry systems, have already received considerable attention from conservation biologist, yet only few of these studies have assessed the impact of agricultural intensification on multiple taxa (De Beenhouwer et al. 2013). However the low levels of traditional crop systems and silvicultural managements decrease the potential for higher yields and other market advantages of tropical agroforestry systems. The evaluation of the productivity on a methodological point of view is also challenging because products issued from these systems are highly diversified. The standardization of the value of these products cannot be overlooked. The evaluation of global productivity is an important step to understand how diversification can be a good option for farmers. Such an approach should help addressing my second specific scientific question:

Question 2

How plant diversity influences the global productivity of agroforestry systems?

Spatial organization of plants could strongly influence the production. Understanding how the spatial organization of diversified plant communities

alters their productivity is an important step in designing and managing diversified agroecosystems (Monzeglio and Stoll 2005). Explaining species performances remains challenging in fields where plant spatial organization is heterogeneous. There is still a need to develop methods to unravel how the spatial structure of diversified plants can alter the productivity of cultivated plants. Spatial organization is an important factor to study, because farmers can manage it and it is an option to optimize the system. First, it requires a precise description of the composition and structure of the agroforestry systems. Then, there is a need to develop innovative methods to disentangle the effect of plant community structure on productivity. This issues it the core of the third scientific question addressed in my thesis:

Question 3

How the spatial structure of the plant community affects yields?

3. Approached proposed

In my thesis, I addressed these three scientific questions using bibliographical analysis to understand the factors that affect the diversity-productivity relationship and using a field study carried out in the region of Talamanca Costa Rica, to understand how plant diversity and its spatial organization alter the productivity of agroforestry systems.

To address the specific question 1, we conducted a meta-analysis on the relationship between plant diversity and system productivity across a wide range of conditions involving different latitudes, climates, and canopy layers; agricultural and natural ecosystems; and annual and perennial crops. In this analysis we used both an effect size of the plant richness on the productivity and the land equivalent

ratio (LER) to evaluate whether productivity was positively or negatively related to plant richness.

To address the specific questions 2, we evaluated the effect of plant species diversity on the yield of agroforestry systems in the region of Talamanca, Costa Rica. We conducted field survey to investigate how the cultivated plant diversity affects global productivity (the overall production of the system) per type of plant species. The production of each individual plant was estimated and converted into income according to local market prices.

To address the specific questions 3, we used a statistical modelling approach, to analyze the effect of the spatial structure of the plant community in the neighborhood on the yield of each cacao tree and on the growth of banana plant. We developed an individual-based analysis to determine i) the distance at which the number of neighboring plants alters the growth of banana plants or the yield of cacao trees, and ii) the magnitude of this neighbourhood effect (see **Figure 3**). We finally discussed how the production of these agricultural systems can be optimized to suggest improvements in spatial structure to increase productivity**.**

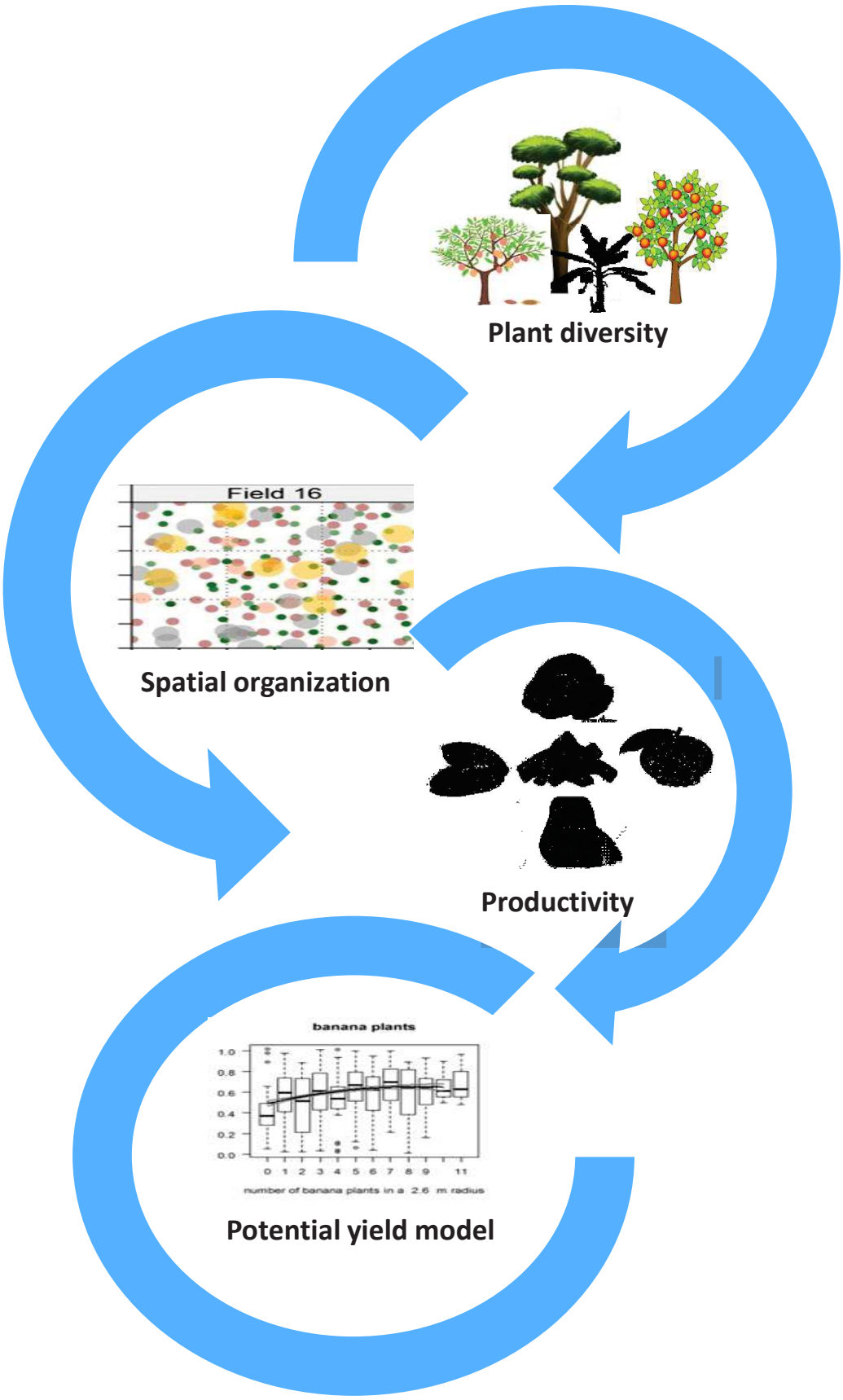

Figure 3. *Disentangle the effect of functional plant diversity and its spatial organization on the agronomic performances of the agricultural systems, taking the case of the region of Talamanca Costa Rica as a model.*

Chapter 2 – General Methodology

In this section, I first present the overall field protocols and then the chosen models to analyze the role of diversity and its spatial organization on the productivity of plants in agroforestry systems.

1. Study area and field protocol

1.1 The Talamanca region

In Costa Rica, one of the more ecologically diverse areas and with presence of diversified cropping systems is Talamanca, which is the largest region in the province of Limón and one of the largest land areas in the country with 576.5 km2. This research was performed in the Bribri indigenous territory, district of Bratsi in Talamanca, Limón Province, south-eastern Costa Rica (9°00′–9°50′ N, 82°35′–83°05′ W). The average annual precipitation is 3570 mm, and the average annual temperature is 25.9˚C. The climate is classified as tropical rain forest (bh-T) (Holdrige 1978). The studied sites could be considered a large share of subsystem such as agroforestry systems that provides environmental services such as soil conservation and biodiversity and improve microclimates. In the role of survival and livelihood, the subsystem produces a wide variety of food and products during all the year, ensuring economic incomes and food security. Food security that has been given independence and autonomy to the Bribri indigenous culture (Guiracocha 2000).

This region presents rich soils, of volcanic origin, with good texture suitable for cacao-banana agroforestry systems, in some parts of the hills. The high content of clay and dense texture confers a less favorable for cropping systems. They are susceptible to erosion events, such as floods and landslides.

Figure *1*. *Geographical location of Bratsi, Costa Rica (Google Maps, 2015)*

The natural environment of the area of Talamanca has been an inherent part of the life of the indigenous Bribris and Cabecares (Boza 2014) . The productivity of farmers in this region is limited by low levels of education, infrastructure, and community development (Borge and Castillo 1997). The spatial design of the architecture of Bribris and Cabécar cropping systems mimic the forest, in which each species has a mythical origin, a story. The association of species follows ancestral rules linked to their functional role (Borge and Castillo 1997).

1.2 The agroforestry systems in Talamanca

In a diagnosis presented by (Somarriba et al. 2014) it is mentioned that cacao plantations in Talamanca agroforest have an average yields between 100 and 200 $Kg.ha^{-1}$ $year^{-1}$. The cacao trees have 3.5-m diameter crowns, intersecting with neighboring plants and thus favoring the emergence of diseases and dissemination of monilia spores (*Moniliophthora roreri*). Most of the cacao trees reach from 6 meters up to 8 meters in height, which make it difficult to perform tasks such as clearing, pruning, removing diseased fruits and harvesting. In

addition many have empty spaces that need to be re-planted. There are useful timber species (dap> 45 cm) of natural regeneration that represents the main sources of wood in the area for the construction of houses and boats. Producers receive from timber and fruit species additional benefits for consumption and sale.

On the other hand, Borge (1997) classified the agroforestry systems in Talamanca according to the banana cropping system; in complex systems (low densities of 156 or 277 plants/ha) and simple systems (higher densities of 1666, 1111 or 833 plants/ha). In the complex systems, low cropping management is done, little sucker removing and deleafing, little weed control (participating to maintain soil moisture and to prevent erosion by rainfall). The simple systems use commercial varieties introduced by the United Fruit Company (UFCO) such as Gros Michel and the Cavendish Lacatan and Congo. These are less resistant than local varieties, to pests and diseases but are much more productive in weight and size. The quantity and diversity of trees is much smaller than in the complex system. There were very few plantain plants within these agroforestry systems, probably because plantains are less tolerant to shade and requires particularly well drained soils (Borge and Castillo 1997).

Although there is a gradient of systems in Talamanca, four types of multi-species systems could be defined:

A- Multi-strata: With more than three timber species remnant from natural forest or from natural regeneration, a canopy with more than three strata. Naturally regenerated timber species present, belong to a small group of successfully reproducing, native species representatives of the local flora, at low population densities (5–20 trees ha^{1}) (Somarriba et al. 2014) in patterns of highly diverse structural and compositional complexity of diversified systems that combine timber species with fruit crops. These agroforests were the most heavily shaded, with almost 93% of shade 1 m above the ground (Deheuvels et al. 2012) with low proportions of weeds.

Figure 2. *Example of a multi-strata cropping system: in an agroforestry system in the region of Talamanca in Costa Rica (photograph by Ricardo Salazar).*

B- Timber and fruits: With more than two timber species remnants from natural forest or from natural regeneration and fruit species, a canopy with more than two strata. Timber species associated mainly with *Theobroma cacao* (cacao) and some other fruit trees as Bactris gasipaes (palm fruit), Citrus sp., (orange) and Persea sp. (Avocado) without any chemical inputs. These agroforests were still heavily shaded, with almost 88% of shade 1 m above the ground (Deheuvels et al. 2012). Musa were almost absent in this system and weeds are presented in low proportions.

Figure 3. *Example of a cacao associated with timber: in an agroforestry system in the region of Talamanca in Costa Rica (photograph by Ricardo Salazar).*

C- Timber and Musa: With more than two timber species remnants from natural forest or from natural regeneration associated with Musa; a canopy with more than two strata. These agroforests had 70% of shade 1 m above the ground (Deheuvels et al. 2012). Their ground cover had a high proportion of weeds.

Figure 4. *Example of a banana associated with timber: in an agroforestry system in the region of Talamanca in Costa Rica (photograph by Ricardo Salazar).*

D- Single strata: These agrosystems are cultivated at the foot of the hill on the river shore, therefore most of them are flooded at least once a year, reason why included almost no tree seedlings. Not more than two species for shade from natural regeneration, one or two strata. Musa are the dominant genus, commercial varieties growing, such as Gross Michel and Cavendish, Lacatan, and Congo. Weeds are presented in high proportions.

Figure 5. *Example of banana single strata: in the region of Talamanca in Costa Rica (photograph by Ricardo Salazar).*

1.3 Selection of plots and data collection

For this thesis, we had the collaboration of APPTA (Asociación de Pequeños Productores de Talamanca) that is an association of small agroecological farmers in Talamanca, conformed by more than 1000 indigenous farmers who are engaged in the production of organic cacao and banana that are marketed in the fair trait market, certificated Bio-Suisse and USDA Organic Farming.

We selected a network of 20 agroforestry fields (**Table 1**) that included a wide range of diversity and spatial organization. Each field was 900 m^2 (30 m x 30 m). The fields were in four villages (Amubri, Dururpe, Katsi, and Watsi) and were located 200-400 m.a.s.l. The farms were selected according to the following criteria: (i) the farmer was available and willing to participate in the research, (ii) the farm area was relatively flat, and (iii) the farm had the potential to produce at least one commercial crop. The selected farms represent indigenous smallholder farms (2 ha on average) in the Talamanca region.

Table 1. Selected plots in the four localities of the study.

# Plot	Farmer	Locality	# Plot	Farmer	Locality
1	MARINA	WATSI	11	ANABELLE	AMUBRI
2	ELSA	WATSI	12	RICARDO	KATSI
3	CARMEN	WATSI	13	ALONSO	KATSI
4	ASDRUBAL	WATSI	14	TONY	KATSI
5	WILFREDO	WATSI	15	MARIA	KATSI
6	SARA	WATSI	16	RUTH	KATSI
7	JOSE MARIA	AMUBRI	17	ISMAEL	KATSI
8	ROSEMARY	AMUBRI	18	LAYAN	DURURPE
9	ELISEO	AMUBRI	19	AMADEO	DURURPE
10	DARIA	AMUBRI	20	ANA	DURURPE

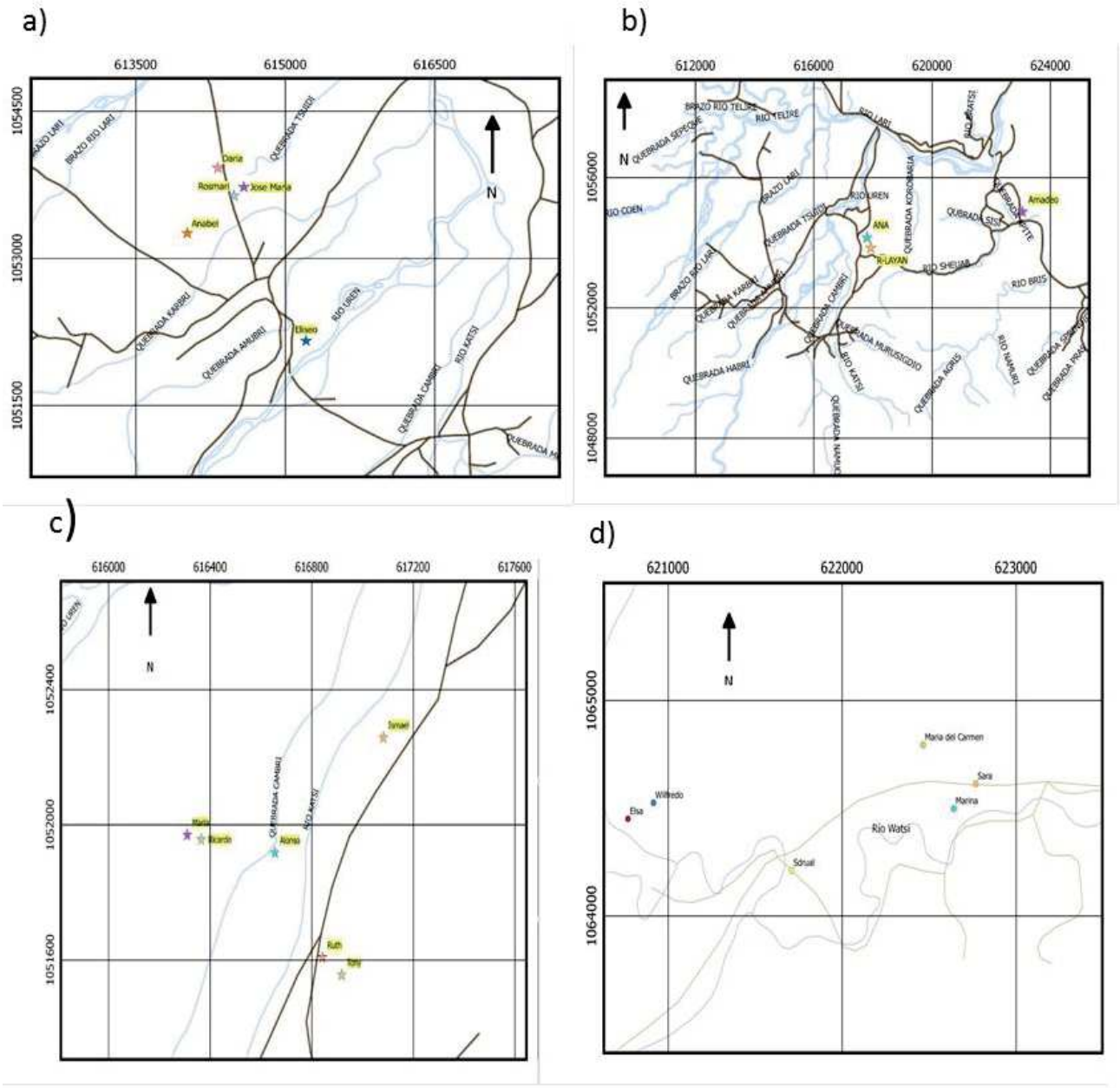

Figure 6. *Geographical representation of the selected plots in the four localities of the study, a) Amubri, b) Dururpe, c) Katsi, d) Watsi*

As show in **Figure 7**, each field was divided into nine plots (10 m X 10 m); the plot was the statistical unit used in one part of the analysis of the study and the individual plants was the statistical unit used in another part of the analysis of the study. We identified and determined the coordinates for all of the cultivated plants (with a commercial value) in all plots. Each plant was tagged, allowing multiple measures over time. Overall, our dataset included 2299 plants. Herbaceous

plants were not recorded. I received assistance to collect the data of two students and two local technicians.

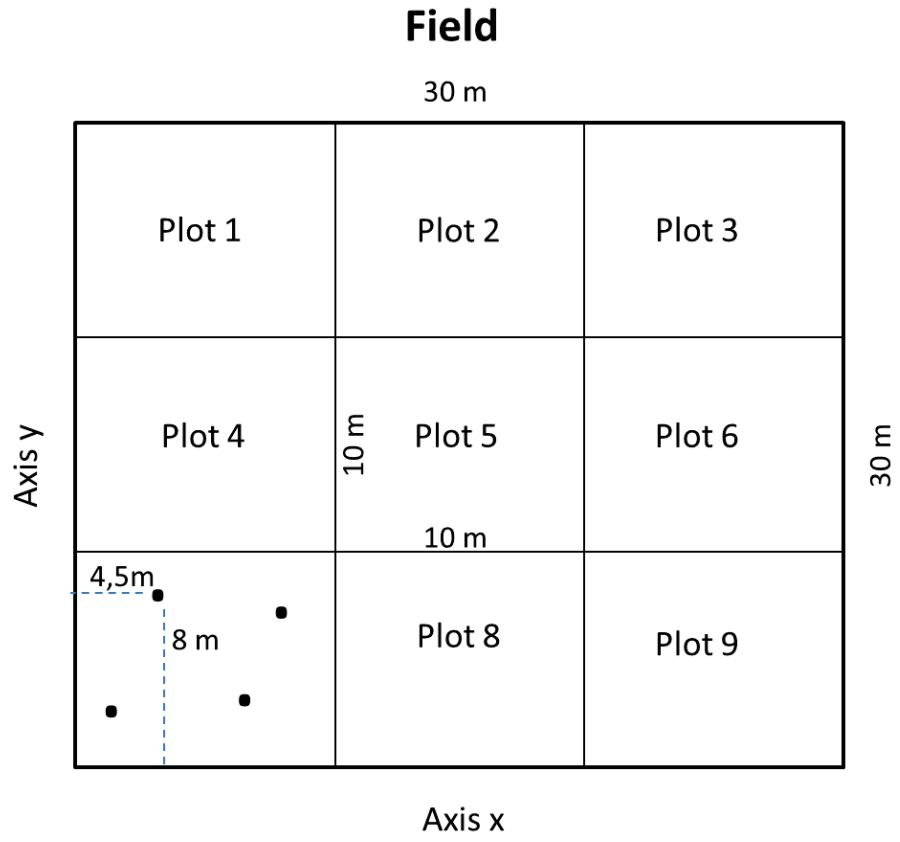

Figure 7. *Example of how we determined the coordinates for all of the cultivated plants (with a commercial value) in 9 plots (10 m X 10 m each plot) of the 20 studied fields (30 m X 30 m each field).*

1.4 Composition of vegetation and spatial structure

These agroforestry systems include as main cash crops: cacao (*Theobroma cacao L.*) and organic banana (*Musa* spp. AAA). Cacao is usually grown with other fruit trees and with shade trees, such as laurel (*Cordia alliodora* Ruiz and Pav.) or cedar (*Cedrela odorata* L.). These shade trees represent species from the natural forest and are either planted or are naturally growing remnants. Banana is an important crash crop for farmers and is usually grown with citrus (*Citrus* spp.), avocado (*Persea americana* Mill.), peach palm (*Bactris gasipaes* Kunth), and other fruit trees. Farmers claim that these other fruit trees grow well with cacao and banana (farmers' personal communication). Other species, such as jicaro (*Crescentia cujete* L.) and senko (*Carludovica palmata* Ruiz and Pav.),

are used for crafts, while guava (*Inga* sp.) and turkey tail (*Cupania cinerea* Poepp.) are used for firewood. **Figure 8** presents an image of the vertical structure of a typical agroforestry system in Talamanca, in which the different strata can be found very well.

Cultivated plant diversity in each plot was calculated using the Shannon–Wiener index, (Shannon 1948), which was calculated with the 'diversity' function of the 'vegan' package, version 2.2-1 (Oksanen et al. 2015).

We also assigned each plant to one of five categories: (i) banana, (ii) cacao, (iii) other fruit trees, (iv) timber, and (v) firewood. Cacao and banana are mainly sold for the international market, while other fruit, timber, and firewood are sold locally or used for self-consumption.

The selected fields have diverse spatial arrangements with different crops densities. We identified and determined the coordinates for all of the cultivated plants (with a commercial value) in each plot. Plants without commercial value (only herbaceous weeds in the lower strata) were not included in this study. Plants with commercial value were identified to either the species or family level and were assigned to one of five categories: banana plants, cacao trees, timber wood trees, firewood trees and fruits trees. Wood trees were the tallest, forming the top canopy layer (with a maximum height of 40 m). The intermediate vegetation layers were represented by fruit trees (with a maximum height of 26 m), and cacao and banana were located in the lower strata (with an average height of 6 m). Plants shorter than 1.5 m were not recorded.

Table 2. The plant taxa measured in this study and their assignment to the five functional groups. Abundance refers to the number of plants in all 20 fields.

	Abundance
Cacao group	
Hybrid	750
Banana group	
Cavendish AAA	340
Grosmichel AAA	277
Lacatan AA	158
Musa spp. AAA	248
Musa spp. AAB	92
Fruits group	
Citrus × sinensis	38
Citrus x paradisi	1
Citrus × tangerina	5
Citrus x aurantifolia	3
Citrus × limonia	2
Bactris gasipaes	32
Persea americana	19
Crescentia cujete	10
Nephelium mutabile	8
Artocarpus communis	7
Averrhoa carambola	5
Licania platypus	5
Eugenia malaccensis	3
Eugenia stipitata	3
Cocos nucifera	2
Annona purpurea	1
Annona muricata	1
Mangifera indica	1
Carica papaya	1
Morinda citrifolia	1
Bixa orellana	1

Group / Taxa	Abundance
Timber group	
Cordia alliodora	178
Cedrela odorata	15
Dipteryx panamensis	3
Hyeronima alchorneoides	1
Chloroleucon eurycyclum	3
Gliricidia sepium	2
Brosimum alicastrum	1
Diphysa americana	1
Enterolobium cyclocarpum	1
Brosimum lactensis	2
Firewood group	
Cupania cinerea	24
Inga edulis	19
Cecropia obtusifolia	2
Erythrina costaricensis	1
Cordia panamensis	8
Palicourea tetragona	2
Croton billbergianus	3
Neea psychotrioides	3
Naucleopsis naga	1
Trichospermum grewiifolium	1
Cordia lucidula	3
Bursera simaruba	2
Miconia trinerve	1
Spondias mombin	2
Cestrum schlechtendalii	1
Alchornea costaricensis	1
Ocotea mollifolia	1

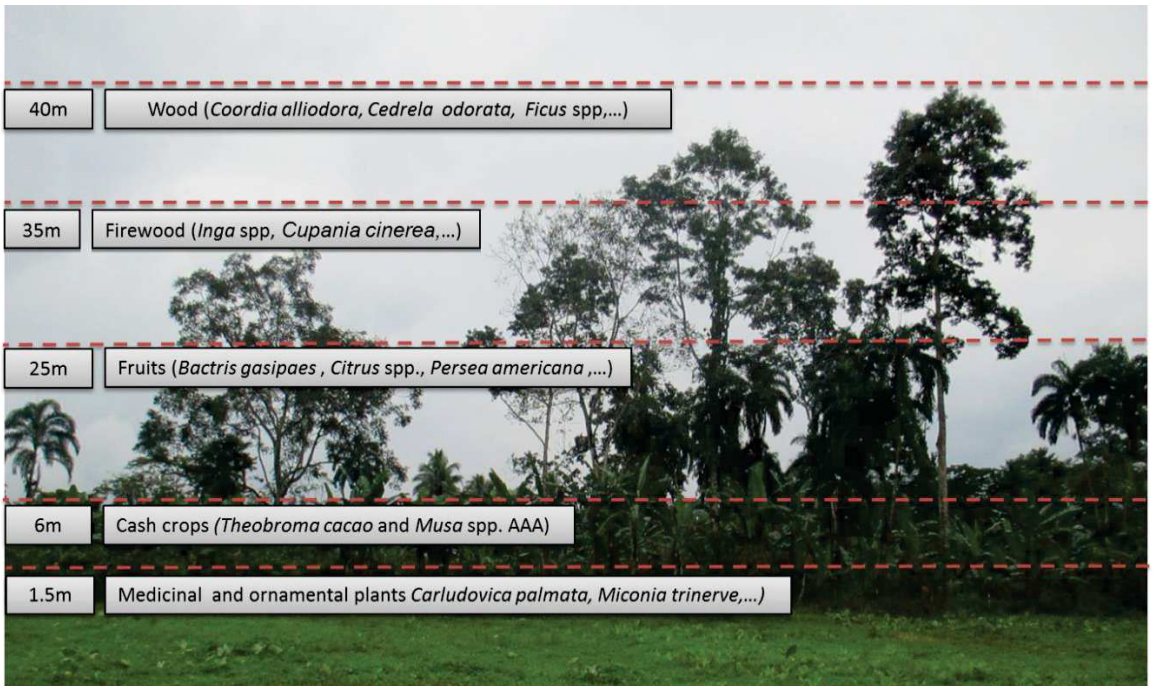

***Figure 8**. Example of the vertical structure of a typical agroforestry system in Talamanca, different strata is indicated with the most common species represented, (photograph by Ricardo Salazar).*

As show in **Figure 9**, the 20 selected plots of agroforestry systems in Talamanca covered a broad range of cultivated diversity, from relatively simple systems (fields 06, 14 and 15) associating one species to banana, to the most complex systems with often more than 20 plant species (fields 16 and 17), they present a multi-strata structuration of the canopy. **Figure 9** show how the spatial structure of the plot could be related with the objective of the farmer in terms of productivity, for example in field 08 there is a remarkable interest for fruit trees, probably related to one species of *citrus* spp for example, in fields 04, 09 and 10 timber species are an important component, in fields 02 and 12 cacao is the most important crop, others fields like 03, 11 and 13 the different crops are very well distributed. Fields like 19 and 20 have a combination of banana and cacao as the main two cash crops.

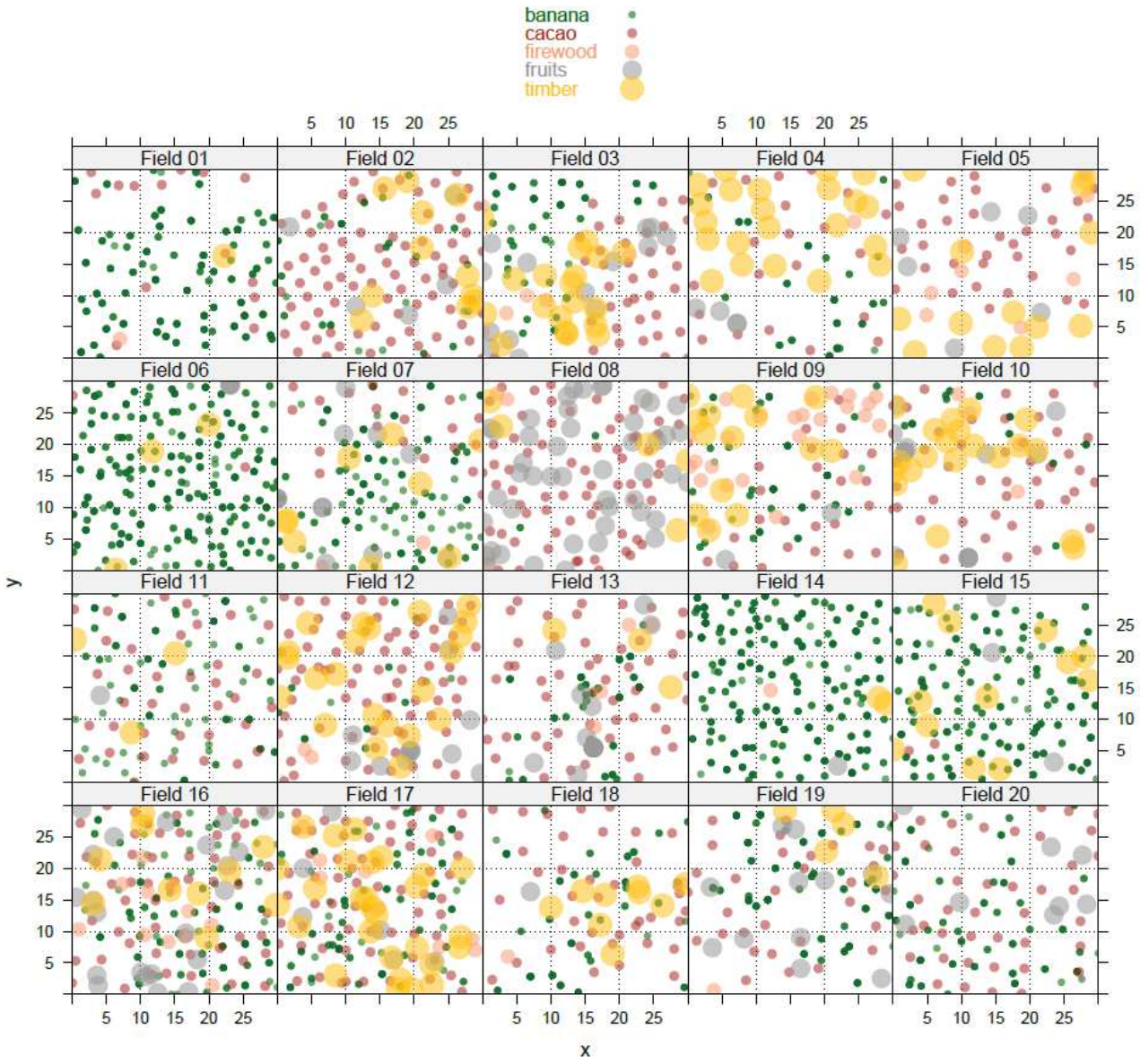

Figure 9. *Maps of the diversity and spatial distribution of individual cultivated plants in the 20 studied plots in Talamanca, Costa Rica. Each plant was assigned to one of the five categories (green: banana plants, brown: cacao trees, grey: fruit trees, pink: firewood trees, yellow: timber trees). The X and Y coordinates are in meters.*

Figure 10 shows the general distribution of densities of plants of each categorical group in the 20 studied plots. Due to the density of crops, there was interest in the production of cacao and banana in all plots (except field 5 witout banana plants). In some of them, there was interest in supplementing production with timber and fruit species. This is in line with what has been reported by several authors (Kapp 1989, Borge and Castillo 1997, Guiracocha 2000, Deheuvels et al. 2012) when referring to the structure of land use in the indigenous area of Talamanca.

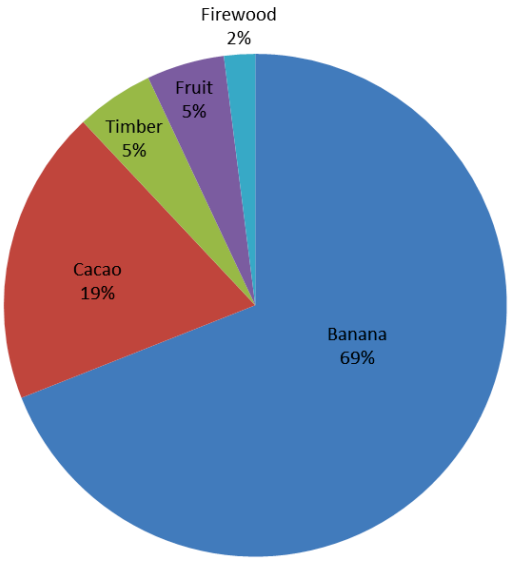

Figure 10. *Distribution of the number of plants of each group in the 20 studied plots in Talamanca, Costa Rica.*

2. Productivity of the agrosystems

The evaluation of productivity in the agroforestry systems in the Talamanca is challenging because of the diversity of the plants that are grown. Guiracocha (2001) reported more than 30 associated tree species in these systems; we identified 56 different commercial species assignment to the five functional groups (see **Table 2**). To estimate the global productivity of the studied fields, we measure the productivity according to our different analysis and to the specification of each functional group presented below.

Banana productivity

Analysis 1 – To estimate banana yield, we measured the weight of bunches and counted their fruits. Every banana plant was followed during 1 year to precisely measure those that were harvested or lost when plants were pruned or toppled-over.

Analysis 2 - To calculate the potential growth for banana plants, we estimated the increase in vegetative biomass during the 17 weeks (in April 2015 and them again in July 2015) by measuring the circumferences of the pseudostem of each plant (1 m above ground level). We assumed that the potential growth of banana followed a parabolic curve, that show how the vegetative growth rate increased up to the reproductive stage and then slightly declined (see **Figure 11**). Similar to classical yield gap analyses, we define an envelope curve that represent the potential yield. The percentage of potential yield for each banana plant was then calculated dividing the measured yield with the potential yield:

$$PPY = \frac{Y\ measured}{Y\ potential}$$

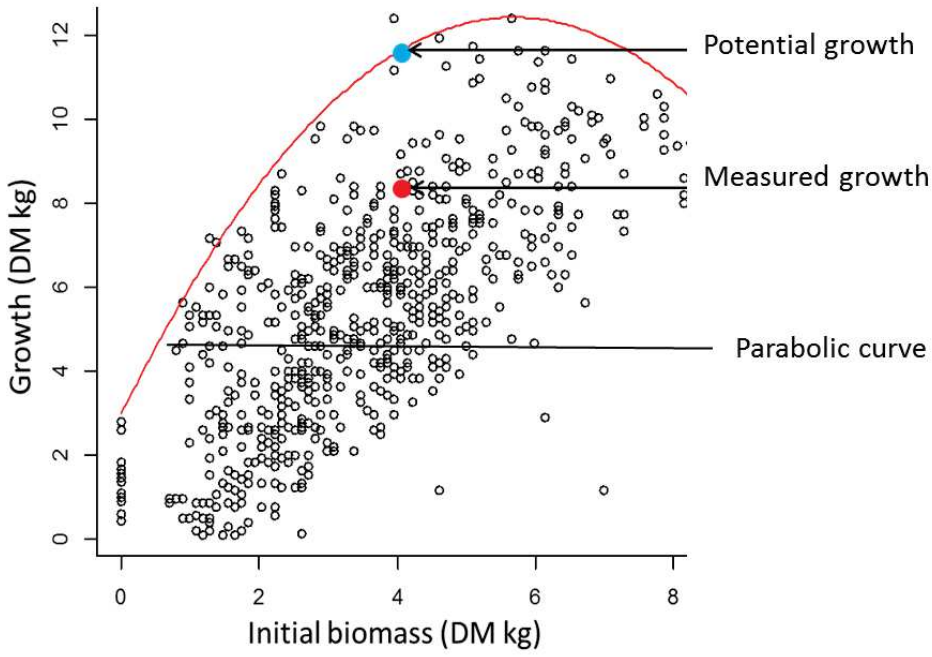

Figure 11. *Example of a parabolic curve followed to determine the potential growth of bananas plants.*

Cacao productivity

Analysis 1 – To estimate cacao yield, we counted healthy cacao pods during the two peak of harvest in May and November. According to Braudeau (1969) cited by (Deheuvels et al. 2012), each pod produces an average of 185 grams of fresh cacao beans that we multiplied by 0.56 (W. Rodriguez personal communication) to estimate the commercial yield of dry cacao.

Analysis 2 – We determined the potential yield for each tree based on the circumference of the tree at 1 m above ground level in April 2015. Similarly to banana plants (see **Figure 11**), we determined the gap between the observed and potential yield for each cacao tree. We assumed that the number of cacao pods increased as the initial tree circumference increased and then greatly decreased following a parabolic curve and that the potential number of pods depended on the tree girth. The potential yield of cacao tree was then calculated as the ratio between the measured number of pods and the potential number of pods for the same girth, similarly to banana PPY.

Timber productivity

For every timber tree, total height, commercial height, and DBH (diameter at breast height) were measured with a hypsometer and a diametric tape. Cubic meters of wood were calculated based on empirical relationships reported by Almendarez et al. (2013) and with a form factor of 0.7 for timber species. With firewood species, we applied the same method using a form factor of 0.5.

Fruit productivity

For other fruits than banana and cacao productivity was estimated for each tree using theoretical values reported by another study in the same region (Burgos et al. 2008).

We estimated the incomes generated by each category of plant according to local market surveys of product prices provided by an association of smallholder farmers from Talamanca (APPTA); the estimates were converted into US dollars. Costs of labour, crop management, and land use were not included in our analysis. The market prices of the products considered in our study were: banana \$0.14/kg, cacao \$2.25/kg, timber \$0.18/m^3 (regardless of species), firewood \$0.03/m^3, and other fruits between \$0.18 and \$1.80/kg depending on the species.

3. Models as tools to analyze the relationship between productivity, cultivated diversity and spatial of plants

We analysed the relationship between productivity and diversity with two points of view:

Analysis 1 - To examine the relationship between the income generated by each group cultivated plants and plant diversity, we used generalized linear mixed-effects models (Bolker et al. 2009). In these models, the plot was the statistical unit used in the study (180 plots), and the field was considered as a random effect.

Analysis 2 - We analysed the effect of the structure of the plant community in the neighbourhood of each individual cacao tree and banana plant on their yield. We used a linear mixed-effect model with the PPY as a response variable and the number of neighboring plants of each category as predictors, the individual plant was the statistical unit used in the study. All models were fitted with the 'lmer' function in the 'lme4' package (Bates et al. 2011). All statistical analyses were performed with R 3.3.0 (R Core Team 2016) and with an alpha level of 0.05.

3.1 Modelling interactions at the local and individual scale

Our aim was to determine the effect of neighboring plants on the potential yield of banana and cacao plants. To this end, we developed an individual-based analysis considering the plot as a random factor, which enabled us to take account for the variability due to the conditions of each plot: pest and diseases, soil, landscape context, and crop management. We carried out the analysis in two steps. First, we determined, without *a priori* assumptions, the distance at which the number of neighbouring plants of a given functional group (banana plants, cacao trees, fruit trees, or wood trees) best explain the potential yield of cacao and banana plants in a GLMM (**Figure 12**).

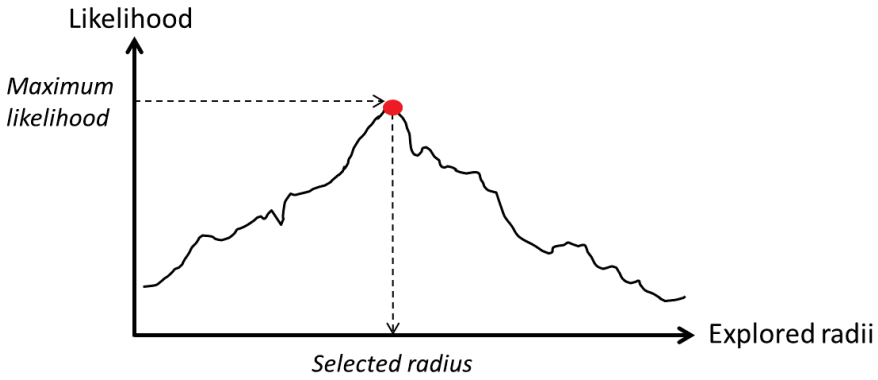

Figure 12. *Likelihood of the model that predicts PPY as a function of the radius at which the abundance of neighboring plants is considered. The distance selected corresponds to the highest values of likelihood observed in the explored range of radii.*

In the second step, we tested the significance of the abundances of the functional groups of plants in a complete model that predicted the PPY of banana and cacao plants.

Chapter 3 – Effect of plant richness on the productivity of multi-species cropping systems

The effect of plant richness on the productivity is often assumed to be a well-known relationship or considered to be characterized in a given condition. However, there is lack of a quantification and comparison of this effect in diverse conditions, especially in agricultural systems. A meta-analysis is a powerful and informative tool to provide a statistical framework for synthesizing and comparing the results of studies which have all tested a particular hypothesis (Harrison 2011). We conducted a meta-analysis to search general rules that link plant richness and the productivity of the agroecosystem. The specificity of our analysis was to disentangle the plant richness – productivity relation according to the climatic area of each study and the type of plants involved in the plant mixtures. Among the hypotheses tested here, this analysis allowed us to question whether the solar radiation resource (supposed to be linked to the latitude) and the vertical structure of the canopy are good predictors of the response of productivity to plant richness. In an agriculture perspective, this meta-analysis aims at identifying the conditions in which plant diversification could generally be a promising option to improve production.

This meta-analysis followed the main steps presented by (Philibert et al. 2012). After a thorough search of articles in Web of Knowledge database and a careful selection of articles that fit meta-analysis requirements, 66 articles were ultimately selected corresponding to 343 experiments.

This study is currently submitted (in revision) in the journal **Agronomy for Sustainable Development**.

Responses of productivity to plant richness: A meta-analysis for diversification of agricultural ecosystems

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Keywords: intercropping, multistrata, productivity, overyield, agroecosystems, plant richness, biodiversity effect.

Abstract. Plant diversification is increasingly presented as a promising way to increase agricultural sustainability. Despite long struggle to understand the mechanisms of coexistence in plants mixtures, it is now certain that knowledge from both ecology and agronomy have to contribute to improve plant productivity in agroecosystems. In this study, we present a meta-analysis that aims to increase our understanding of how plant richness alters the productivity under a wide range of factors (latitude, climate, canopy structure) across annual and perennial plant diversity experiments in agricultural and natural ecosystems. The 66 selected articles included 343 experiments. For each experiment, we extracted all of the information on potential predictor variables; we used both, the land equivalent ratio (LER) and the effect size (Z), to assess the response of productivity to plant richness in the broad range of effects. Overall, productivity was strongly and positively correlated with plant richness. However, the gain per unit of diversity added decreased as plant richness increased. We found that LER values decreased with latitude and suspect that the availability of solar radiation, which decreases with latitude, might alter the relationship between plant richness and productivity. Our findings also showed that the response of productivity to plant richness largely depends on the type of plants in the community. The presence of trees in the canopy reduced the effect of plant richness on productivity but also reduced the variability in the relationship, suggesting that trees may help stabilize productivity. From an agricultural perspective, our results suggest that productivity could be maximized by a relatively low number of plant species.

1. Introduction

Intensive agriculture of the 20th century is associated with an intensification and simplification of agricultural practices with the aim to increase yield, often in detriment of biodiversity, affecting both wild species whose habitat disappeared and cultivated species whose genetic diversity was often greatly reduced (Tilman et al. 2002). Biodiversity in agroecosystems is now a major concern and promises to be a major issue of the 21st century (Plantureux et al. 2005, Isbell et al. 2015a). .The diversification of agricultural systems can be achieved through a variety of options ranging from the intercropping of two species to the assembly of very complex systems that mimic nature (Altieri 2002, Malézieux et al. 2009). The effect of plant diversity on productivity has long been studied in natural systems (Naeem et al. 1994, Loreau et al. 2001), but there is still debate about how plant diversity can be increased in agricultural systems without decreasing productivity and making management too difficult for farmers (Swift et al. 2004). There is thus a need to understand the type of plant to be used for the diversification of agricultural ecosystems and the optimal degree of diversification. (Huston 1997, Tilman 1997, Loreau 1998, Hector et al. 1999, Malézieux 2012)

Positive effects of species richness on yield in agroecosystems, and on biomass production in natural ecosystems, have been shown to arise due to two types of mechanisms: sampling effects and complementarity between species (that include both niche differentiation and facilitation because distinguish between them is difficult in practice) (Loreau and Hector 2001). Recent meta-analyses underlay the important potentially role of these mechanisms on overyielding in experimental plant mixtures. For instance, Li et al. (2014) have shown that plant diversity may enhance productivity by facilitation of nutrients acquisition in annual and herbaceous perennial intercropping systems. Craven et al. (2016) also found that the diversity and complementarity of species are important regulators in grassland ecosystem productivity. Yu et al. (2015), who studied how the productivity of mixed cropping systems is affected by intercropping system design and species traits, reported that crop diversity can substantially enhance productivity. In a field experiment, Fridley (2003) found that the effects of diversity on productivity depended on fertility and that overyielding in diversified systems was only evident under conditions of high fertility. According to Mulder et al.

(2001), environmental stresses favor positive relationships between plant species richness and productivity; suggesting stresses limit the importance of competition. However, a recent meta-analysis rejected the stress-gradient hypothesis (stating that stress enhances facilitation between neighbors) and concluded that neither positive nor negative effects of neighbors increased with abiotic stress because species interactions across abiotic stress gradients do not follow a simple pattern (Maestre et al. 2005). While the effect of plant diversity received a great attention in others meta-analysis (Cardinale et al. 2007, Yu et al. 2015, Craven et al. 2016) different environmental gradients have been neglected, our analysis is important because it cover a wide gradient of ecosystems in a wide range of environmental conditions.

The diversity-productivity relationship is expected to change with environmental context (Cardinale et al. 2000). Fridley (2002) even suggested that the local environmental factors should have a much stronger effect on local ecosystem functions than the diversity of the species pool. The climate is the primary driver of these conditions, it is thus crucial to analyze the richness-productivity relationship taking climate into account. Other factors including the type of plants (Lavorel et al. 1997) and the canopy structure (Grime 1998) are also major drivers that need to be considered when analyzing this relationship. Our aim was to define the conditions favorable to plant diversification in agroecosystems, we thus included these different factors in our analysis.

In this article, we conducted a meta-analysis on the relation between plant diversity and system productivity considering the effect of latitude, climate, and number of strata in the canopy across a wide range of annual and perennial plant diversity experiments in agricultural and natural ecosystems. To assess the response of productivity to plant richness, we used both, the land equivalent ratio (LER) and the effect size, to cover a broad range of plant diversity effects. These two complementary indicators were used to investigate the following questions: (1) does the relationship between plant diversity and productivity differ between agricultural systems and natural systems? (2) How do latitude and climate affect the plant richness-productivity relationship? (3) How does canopy structure affect the plant diversity-productivity relationship? (4) Does the relationship between

plant diversity and productivity differ depending on the type of plants in the system?

2. Methods

2.1 Review and study selection

In November 2016, we selected articles through a literature search on the Web of Science Core Collection and using the following search terms: (“overyield” OR “intercrop”) AND (“plant diversity” OR “plant richness”). Over 500 abstracts were reviewed for relevance, and 66 articles were ultimately selected using the criterion that they contained data on the relationship between plant diversity and productivity. These articles were published between 1993 and 2016.

The 66 selected articles reported on 343 experiments. For each experiment, we extracted all of the information on: i) potential predictor variables (independent variables) and ii) response variables (dependent variables) that characterize the effect of plant richness on the productivity: the land equivalent ratio (LER) and the effect size.

2.2 Response variables

The LER is the sum of the relative yields of component species in an intercrop as compared to their respective sole crop. The effect size was calculated to estimate the magnitude of the relationship between the variable and its response to productivity when LER is not reported. the LER was calculated as the sum of the relative yields of component species in an intercrop as to their respective sole crops (Yu et al. 2015).

LER is defined as:

$$LER = \frac{Y1}{M1} + \frac{Y2}{M2}$$

where Y1 and Y2 are the yields (per unit of total areas of the intercrops) of species 1 and 2 when intercropped, and M1 and M2 are the yields of the species in monoculture (per unit area of the respective single crop).

Effect size estimates the magnitude of the relationship between a predictor variable and its response using any test statistic derived from independent research studies. It is a statistics that provide a standardized, directional measure of the mean change in the dependent variable in each study (Harrison 2011). The effect size was estimated with the Fisher's Z, which was defined using the equation of Rosenthal and DiMatteo (2001).

$$\mathrm{Z} = \frac{1}{2}\log[(1 + \mathrm{R}/(1 - \mathrm{R})]$$

The sign of R was deducted from the sign of the effect in the studies. To compute Fisher's Z, we converted the test statistic (df, P, t, or R^2) from each response reported in a study to the correlation coefficient R as a standard statistic. The coefficient R of correlation was directly extracted from the studies, calculated from R^2, or calculated from n the number of data and t the value of the Student test of each response following:

$$R = \sqrt{\frac{1}{\frac{n-2}{t^2} + 1}}$$

2.3 Predictor variables

In the analyses, we defined five categorical predictor variables: (i) ecosystem (natural or agricultural); (ii) climate (tropical, subtropical, temperate, continental, or semi-arid); (iii) plant duration (annual or perennial); (iv) plant type (vegetables/legumes, grains/cereals, perennial grass, agroforestry, natural forests), and (v) strata number (i.e., number of canopy layers). We also defined two continuous predictor variables: latitude and magnitude of plant richness. Magnitude of plant richness was the maximal number of plant species present in a defined geographical unit.

2.3.1 Predictor variables classification

We classified data from the relevant selected papers according to seven predictors:

(1) The magnitude of plant richness (continuous variable): number of plant species growing together reported in experiments.

(2) The latitude (continuous variable).

(3) The type of system: natural ecosystem or agricultural system. We considered natural and planted forest experiments as natural ecosystem and intercropping of annual plants, perennial grass and agroforestry experiments as agricultural system.

(4) The climate type: based on the Köppen-Geiger system (Peel et al. 2007).

(5) The annual and perennial status of plants: determined based on the phenology of plants (Rathcke and Lacey 1985). Perennials grass mixtures were classified as perennial.

(6) The cropping system type: seven groups were defined (vegetables, legumes, grains, cereals, perennial grass, agroforestry, forests).

(7) The number of strata layers in the canopy:

- i) one stratum (for vegetables, legumes and some grains, cereals mixtures),
- ii) two strata (for perennial grass and some grains, cereals mixtures),
- iii) three (or more) strata (for agroforestry and forest).

2.4 Statistical analysis

Using the data from the 343 experiments in the 66 studies, we generated 95 effect sizes (Z values) and 248 LER values. We used the generalized linear model (GLM) to test the significance of predictors on the LER and on the effect size Z. Statistical analyses were performed with R 3.3.1 (R Core Team 2016) and with an alpha level of 0.05. On most relevant models, we carried out a sensitivity analysis by removing separately the responses from each studies and assessing how the estimate of the factors (plant richness and latitude) were altered. We also conducted an analysis of the bias of publication searching whether the number of citation of each study was correlated (linear model) with the effect size Z or with the LER.

3. Results

3.1 General features of the studies

The 66 studies used in our meta-analysis were published within the past 23 years (Table 1) and were conducted in different countries located between 70°N and 40°S latitude. 12 studies were conducted in the Southern Hemisphere and 54 in the Northern Hemisphere. Most of the studies appeared in 32 journals, with 36 falling in the domain of agronomy and 30 in ecology. Of the 66 studies, 10 were conducted in multi-strata ecosystems and 56 were conducted in mono-strata ecosystems.

We retrieved a total of 343 productivity responses to plant diversity. Of the productivity responses, 248 from 36 studies were expressed as LER values, and 95 from 30 studies were expressed as effect size.

Table 1. Background information for the 66 selected studies for the meta-analysis, that characterize the effect of plant richness on the productivity, using the extracted information on the potential predictor variables (Plant richness, Ecosystem, Latitude, Climate, Plant type, Crop system, Strata level) and the number of LER or Z values responses. Plant richness represents maximum number of plant species in the system.

	Plant richness	Ecosystem	Latitude	Climate	Plant type	Crop system	Strata level	LER	Z
(Agegnehu et al. 2006)	2	agricultural	9'03'N	Tropical	annual	cereal	1	5	-
(Andersen et al. 2005)	3	agricultural	55'4'N	Temperate	annual	cereal	1	8	-
(Baldé et al. 2011)	2	agricultural	16'23'S	subtropical	annual	grain	1	4	-
(Holger Bessler et al., 2009)	16	agricultural	50'96'N	Temperate	perennial	grass	2	-	3
(Biondini 2007)	50	agricultural	46'33'N	Continental	perennial	grass	1	-	3
(Bisseleua et al. 2009)	11	agricultural	2'35'S	Tropical	perennial	agroforestry	3	-	1
(Bonin and Tracy 2012)	2	agricultural	37'12'N	subtropical	perennial	grass	1	-	4
(Borer et al. 2012)	16	agricultural	45'4'N	Continental	perennial	grass	1	-	1
(Byrnes et al. 2014a)	18	agricultural	45'45'N	Temperate	perennial	grass	1	-	2

(Chu et al. 2004)	2	agricultural	32'03'N	Semiarid	annual	grain	1	2	-
(Craine et al. 2003)	12	agricultural	45'41'N	Continental	perennial	grass	1	-	2
(de Aguiar et al. 2013)	5	agricultural	3'41'S	Tropical	perennial	agroforestry	3	-	2
(Dhima et al. 2007)	2	agricultural	40'32'N	subtropical	annual	cereal	1	8	-
(Dodd et al. 2004)	8	agricultural	37'48'S	subtropical	perennial	grass	1	-	2
(Echarte et al. 2011)	2	agricultural	37'45'S	Temperate	annual	grain	1	11	-
(Elba et al. 2014)	2	agricultural	37'2'S	Temperate	annual	grain	1	1	-
(Erskine et al. 2006)	3	agricultural	18'51'S	Tropical	perennial	forest	3	-	1
(Franco et al. 2015)	2	agricultural	20'37'N	Semiarid	annual	vegetables	1	10	-
(Fridley 2003)	7	agricultural	35'9'N	subtropical	perennial	grass	2	-	1
(Gao et al. 2014)	2	agricultural	40'54'S	Semiarid	annual	grain	1	3	-
(Ghosh 2004)	2	agricultural	21'31'N	Semiarid	annual	cereal	1	5	-
(Hauggaard-Nielsen and Jensen 2001)	2	agricultural	55'41'N	Temperate	annual	grain	1	12	-
(Hauggaard-Nielsen et al. 2001)	2	agricultural	55'41'N	Temperate	annual	grain	1	3	-
(Hauggaard-Nielsen et al. 2009)	2	agricultural	55'4'N	Temperate	annual	grain	1	14	-
(Hauggaard-Nielsen et al. 2006)	2	agricultural	55'4'N	Temperate	annual	grain	1	2	-
(He et al. 2013)	2	agricultural	23'18'S	subtropical	annual	grain	1	5	-
(Hector et al. 2010)	16	agricultural	47'N	Temperate	perennial	grass	1	-	1
(Hector et al. 2011)	16	natural	5'N	Tropical	perennial	planted trees	3	-	1
(Kahmen et al. 2005)	78	natural	50'24'N	Temperate	perennial	grass	1	-	1
(Karpenstein-Machan and Stuelpnagel 2000)	3	agricultural	51'41'N	Temperate	annual	grain	1	6	-
(Lamošová et al. 2010)	8	agricultural	49'45'N	Continental	perennial	grass	1	-	4
(Lanta and Lepš 2007)	16	agricultural	49'92'N	Temperate	perennial	grass	1	-	3
(Laossi et al. 2008)	4	agricultural	5'16'S	Tropical	annual	grass	1	-	4
(Li et al. 1999)	2	agricultural	37'5'N	Continental	annual	vegetables	2	2	-
(Li et al. 2009)	2	agricultural	25'22'N	subtropical	annual	grain	1	8	-
(Lithourgidis et al. 2011)	2	agricultural	40'39'S	subtropical	annual	cereal	1	6	-
(Mao et al. 2012)	2	agricultural	38'37'N	Continental	annual	grain	1	8	-
(Mei et al. 2012)	2	agricultural	38'37'N	Continental	annual	grain	1	5	-
(Méndez et al. 2009)	20	agricultural	13'54'N	subtropical	perennial	agroforestry	3	-	1
(Midmore 1993)	2	agricultural	22'59'N	subtropical	annual	vegetables	1	6	-
(Nassab et al. 2011)	2	agricultural	48'12'N	Temperate	annual	grain	1	25	-
(Neugschwandtner and Kaul 2014)	2	agricultural	48'14'N	Temperate	annual	cereal	1	8	
(Neto et al. 2012)	3	agricultural	5'11' S	Semiarid	annual	vegetables	1	4	-
(Ni et al. 2007)	8	natural	45'25'N	Temperate	perennial	grass	1	-	1
(Peeters et al. 2003)	13	agricultural	16'75'N	Tropical	perennial	agroforestry	3	-	2
(Pelzer et al. 2012)	2	agricultural	48'8'N	Continental	annual	cereal	1	2	-
(Piper 1998)	3	agricultural	38'44'N	Continental	perennial	grass	1	-	1

(Qin et al. 2013)	2	agricultural	37'96'N	Continental	annual	grain	1	2	-
(Ravenek et al. 2014)	60	agricultural	50'95'N	Temperate	perennial	grass	2	-	4
(Romero-Alvarado et al. 2002)	5	agricultural	26'03'N	subtropical	perennial	agroforestry	3	-	1
(Roscher et al. 2011)	60	natural	55'55'N	Temperate	perennial	grass	3	-	10
(Rusinamhodzi et al. 2012)	2	agricultural	18'46'S	Tropical	annual	grain	1	16	-
(Sadeghpour et al. 2013)	2	agricultural	35'48'N	Semiarid	annual	cereal	1	2	-
(Sanderson 2010)	7	agricultural	41'81'N	Temperate	perennial	grass	1	-	4
(Seidel et al. 2013)	3	natural	51'05'N	Temperate	perennial	forest	3	-	1
(Stoltz and Nadeau 2014)	2	agricultural	56'1'N	Temperate	annual	grain	1	3	-
(Van Eekeren et al. 2010)	2	agricultural	51'39'N	Temperate	perennial	grass	1	-	1
(Vilà et al. 2013)	3	natural	50'44'N	Continental	perennial	forest	3		11
(Worster and Mundt 2007)	2	agricultural	44'48'N	Temperate	annual	cereal	1	-	20
(Wu et al. 2012)	2	agricultural	25'22'N	subtropical	annual	grain	1	6	-
(Yang et al. 2013)	2	agricultural	23'8'N	subtropical	annual	cereal	1	21	-
(Yang et al. 2011)	2	agricultural	37'52'N	Continental	annual	grain	1	9	-
(Zhang et al. 2011)	2	agricultural	36'09'N	Temperate	annual	grain	1	12	-
(Zhang et al. 2004)	2	agricultural	36'09'N	Semiarid	annual	grain	1	2	-
(Zhang et al. 2007)	2	agricultural	36'07'N	Semiarid	annual	cereal	1	12	-
(Zhu et al. 2010)	16	agricultural	29'53'N	subtropical	annual	vegetable	1	-	4

3.2 Global effects of plant richness on plant productivity

Overall, productivity showed a strong, positive response to plant richness, with a similar trend for effect size (**Figure 2A**) and LER (**Figure 3A**). All statistical results are presented in **Table 2**. Interestingly, there was a negative relationship between the effect size and the magnitude of plant richness (**Figure 1A; Table 2**). The relationship between LER and the magnitude of the plant richness also tended to be negative but was not statistically significant (**Figure 1B**). There were more productivity responses from agricultural systems (318 responses) than from natural ecosystems (25 responses), and the response of productivity to plant richness differed between the two systems (**Figure 2B**) with a strong significant

positive response for agricultural systems and a neutral response for natural systems (**Table 2**).

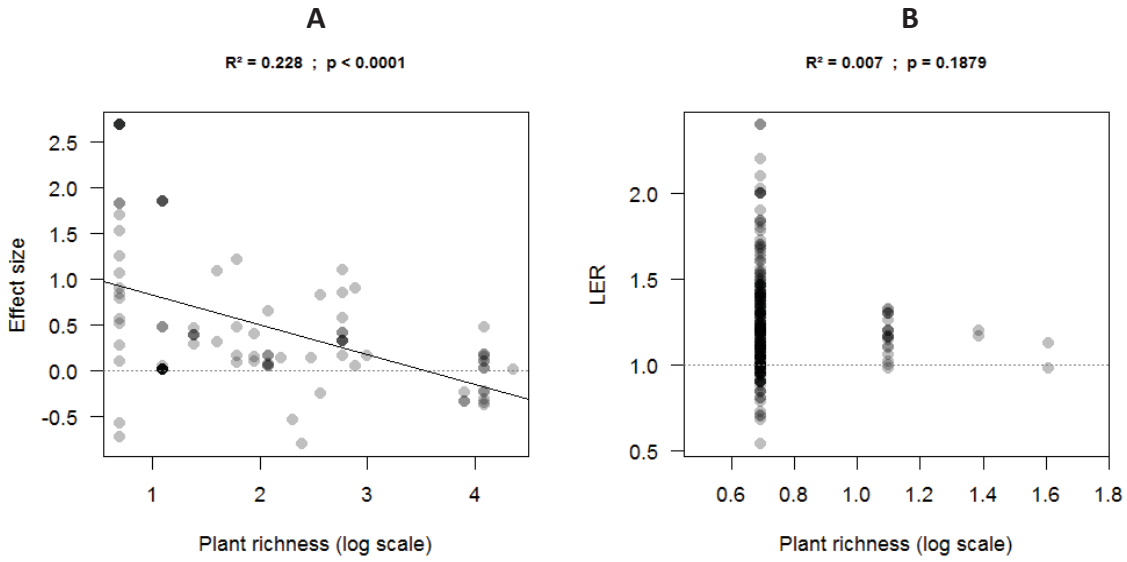

Figure 1. *Response of the effect of plant richness (log scale) on productivity, as evaluated based on the effect size (A) and the LER (B). The horizontal dotted lines indicate the neutral effect.*

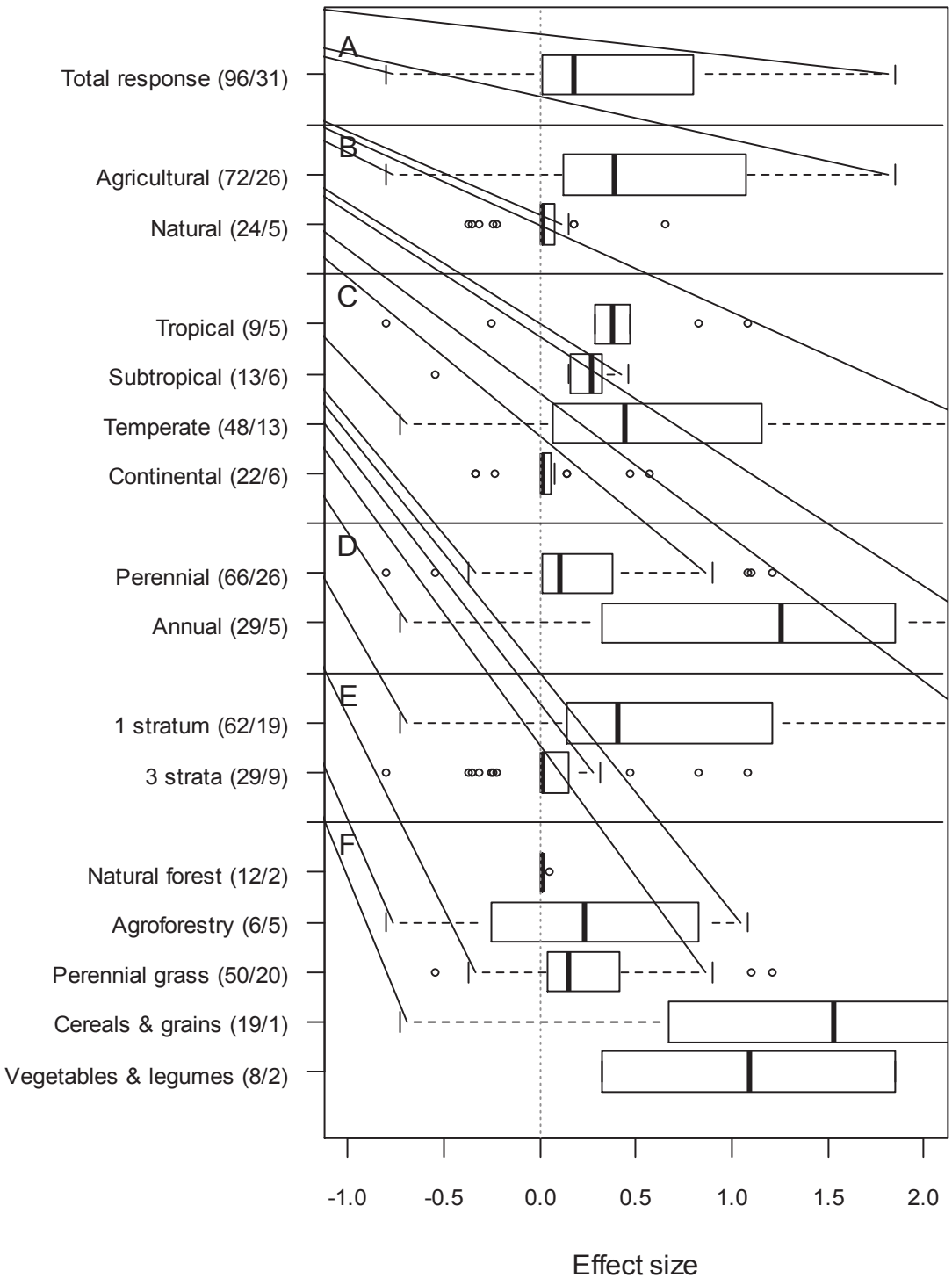

Figure 2. *Boxplot of the plant productivity response to plant richness estimated though the effect size (calculated using 96 responses from 31 studies). For each category, the vertical black bar shows the median value of the effect size, the box show the upper and lower limits of its 25% quartiles and the whiskers show its maximum and minimum values excluding outliers. The numbers in parentheses indicate the total number of responses/total number of studies included in each category. The vertical grey dotted line indicates the neutral effect.*

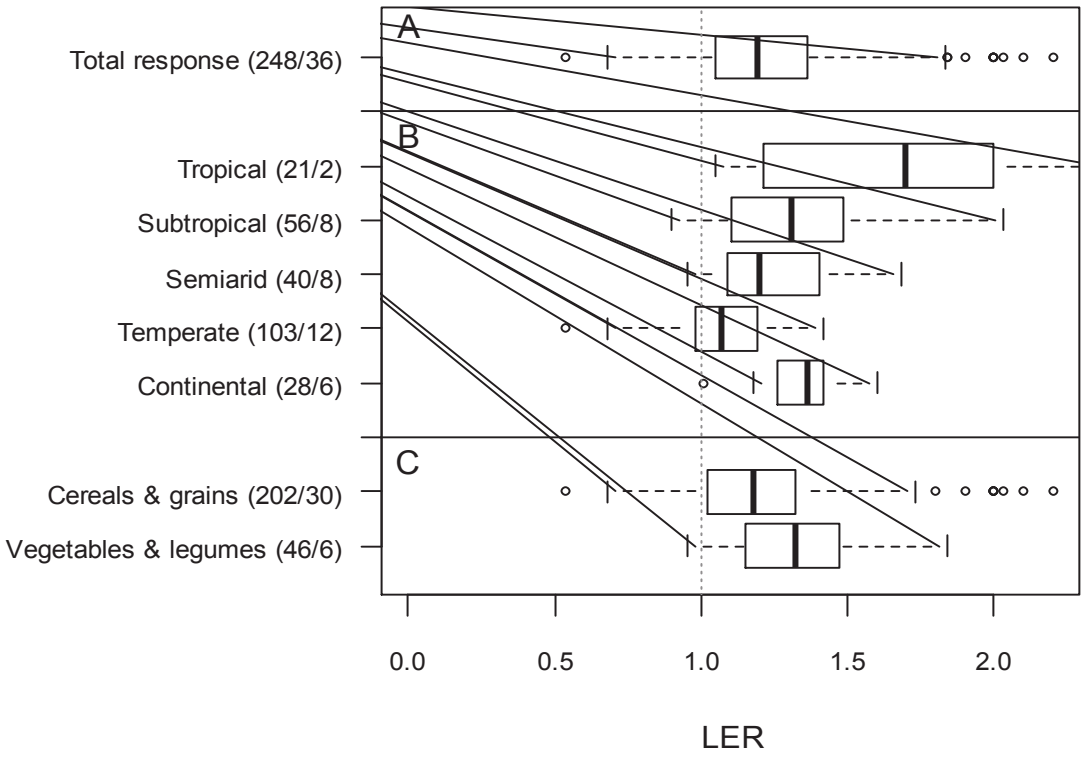

Figure 3. *Boxplot of the plant productivity responses to plant richness estimated with the LER from 248 responses from 36 studies. For each category, the vertical black bar shows the median value of the effect size, the box show the upper and lower limits of its 25% quartiles and the whiskers show its maximum and minimum values excluding outliers. The numbers in parentheses indicate the total number of responses/total number of studies included in each category. The vertical dotted line indicates the neutral effect.*

Table 2. Statistics of the linear models that were used to determine the effects of the plant richness on the effect size and LER as affected by the predictor variables (Ecosystem, Climate, Plant type, Crop system, Strata level).

Grouping factor	df	F	p	r
Effect size response to plant richness				
Total response	94	27.72	<0.0001	-0.48
Agricultural	70	28.15	<0.0001	-0.54
Natural	22	1.52	0.2301	-0.25
Tropical	7	1.36	0.2822	-0.40
Subtropical	11	0.09	0.7722	-0.09
Temperate	46	25.49	<0.0001	-0.60
Continental	20	3.45	0.0779	-0.38
Perennial	64	5.18	0.0262	-0.27
Annual	27	5.28	0.0296	-0.40
1 stratum	60	26.94	<0.0001	-0.56
3 strata	27	1.57	0.2209	-0.23
Natural forest	nc	nc	nc	nc
Agroforestry	4	0.73	0.4411	-0.39
Perennial grass	48	13.79	0.0005	-0.47
Cereals & grains	nc	nc	nc	nc
Vegetables & legumes	nc	nc	nc	nc
LER response to plant richness				
Total response	246	1.75	0.1877	-0.08
Tropical	nc	nc	nc	nc
Subtropical	nc	nc	nc	nc
Semiarid	38	5.76	0.0214	-0.38
Temperate	101	11.46	0.0010	0.32
Continental	nc	nc	nc	nc
Cereals & grains	200	0.03	0.8681	-0.01
Vegetables & legumes	44	10.28	0.0025	-0.46

df: residual degrees of freedom; F: F value of the Fisher test; p: p value of the linear model; r: correlation coefficient, nc: not calculated.

3.3 Effect of "abiotic conditions" on the response of productivity to plant richness

Our results showed a negative response of LER to latitude (**Figure 4B**, df=246, F=65.61, P=<0.0001). This relationship was not significant for effect size (**Figure 4A**, df=83, F=1.657, P=0.2015). Productivity responses to plant richness differed among climatic region (**Figure 2C** and **3B**). The effect size was significantly altered by plant richness in regions with subtropical and continental climates, while the LER was significantly altered by plant richness only in regions with a tropical climate (**Table 2**). Over the entire data set, the response of productivity in terms of both effect size and LER to plant richness tended to be stronger in regions with a tropical climate than in those with other climates.

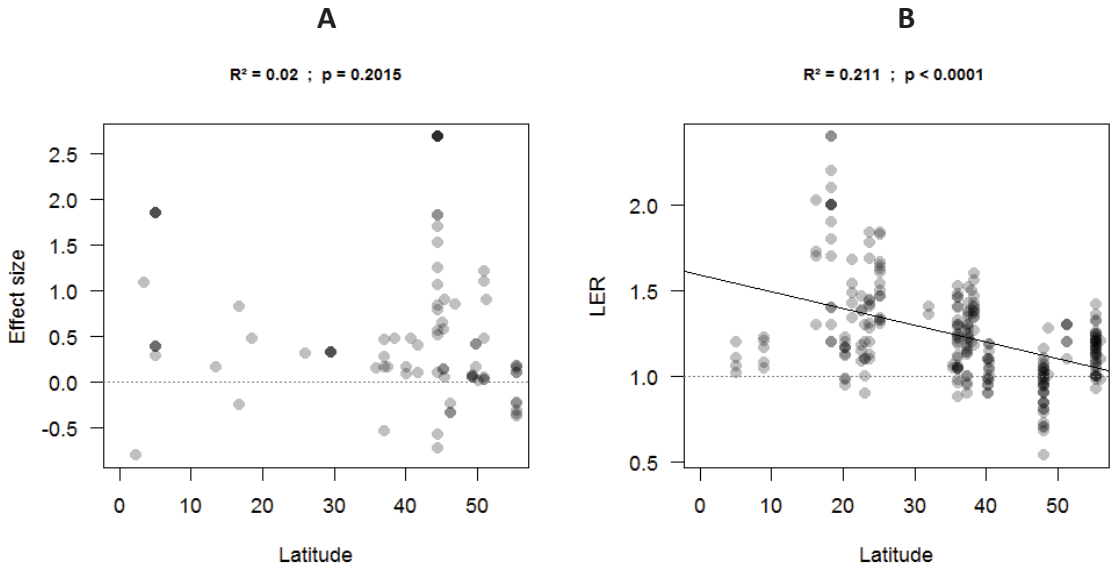

Figure 4. *Effect of latitude (absolute values) on the response of plant productivity to plant diversity, as evaluated based on the effect size (A) and the LER (B). The horizontal dotted lines indicate the neutral effect.*

3.4 Effects of the "plant type" and canopy structure on the response of productivity to plant richness

The effect size was smaller in study systems with perennial plants than in those with only annual plants (**Figure 2D**). This was confirmed by the larger effect size

when ecosystems included only one stratum (as is typical for systems with only annual plants) rather than multiple strata (as is typical for systems with perennial plants) (**Figure 2E**). In line with these results, effect sizes were larger for systems with cereals/grains and vegetables/legumes than for agroforestry or perennial grass systems (**Figure 2F**), although variation in the effect size was smaller for the latter systems. The LER values tended to be higher for systems with cereals/grains than for those with vegetables/legumes (**Figure 3C**). The response of productivity (in terms of LER) to plant richness was significant but negative for vegetable/legume systems (**Table 2**).

Finally, we tested the effect of plant richness, latitude, type of cropping system, and canopy structure on the effect size and the LER in two complete linear models. Interestingly, there was a significant interaction between plant richness and the presence/absence of perennial plants in the system (**Table 3**). Model predictions confirmed that the effect size of plant richness declined as the magnitude of plant richness increased and that the decline was faster for systems with only annual plants than for systems that included perennial plants (**Figure 6A**). In the complete model that predicted LER values, the effect of latitude was highly significant, the plant richness effect was barely significant, and the type of cropping systems was not significant (**Table 3**). The standard error of this model progressively increased with plant richness (**Figure 6B**).

The effect of plant richness on Z and LER was not altered by study removal (**Figure 5**). There was no bias of publication (number of citation of each article) for Z ($p=0.081$) but it was slightly significant for LER ($p=0.022$ with an estimate of 0.0016).

Table 3. Statistics of the complete linear models that were used to determine the effects of plant richness, latitude, the presence of perennial plants, and ecosystem (natural vs. agricultural) on the effect size and LER.

	df	SS	F	p
Effect size response				
Latitude	1	1.18	2.79	0.0990
Plant richness	1	18.58	44.00	<0.0001
Annual/Perenial	2	5.41	6.41	0.0026
Natural/Agricultural	1	0.02	0.04	0.8343
Plant richness : Annual/Perenial	1	1.99	4.71	0.0331
Residuals	78	32.94		
LER response				
Latitude	1	4.29	66.00	<0.0001
Plant richness	1	0.21	3.21	0.0443
Annual/Perenial	1	0.02	0.26	0.6112
Residuals	244	15.85		

df: degrees of freedom; SS: sum of squares; F value of the Fisher test; p: p value of the linear model.

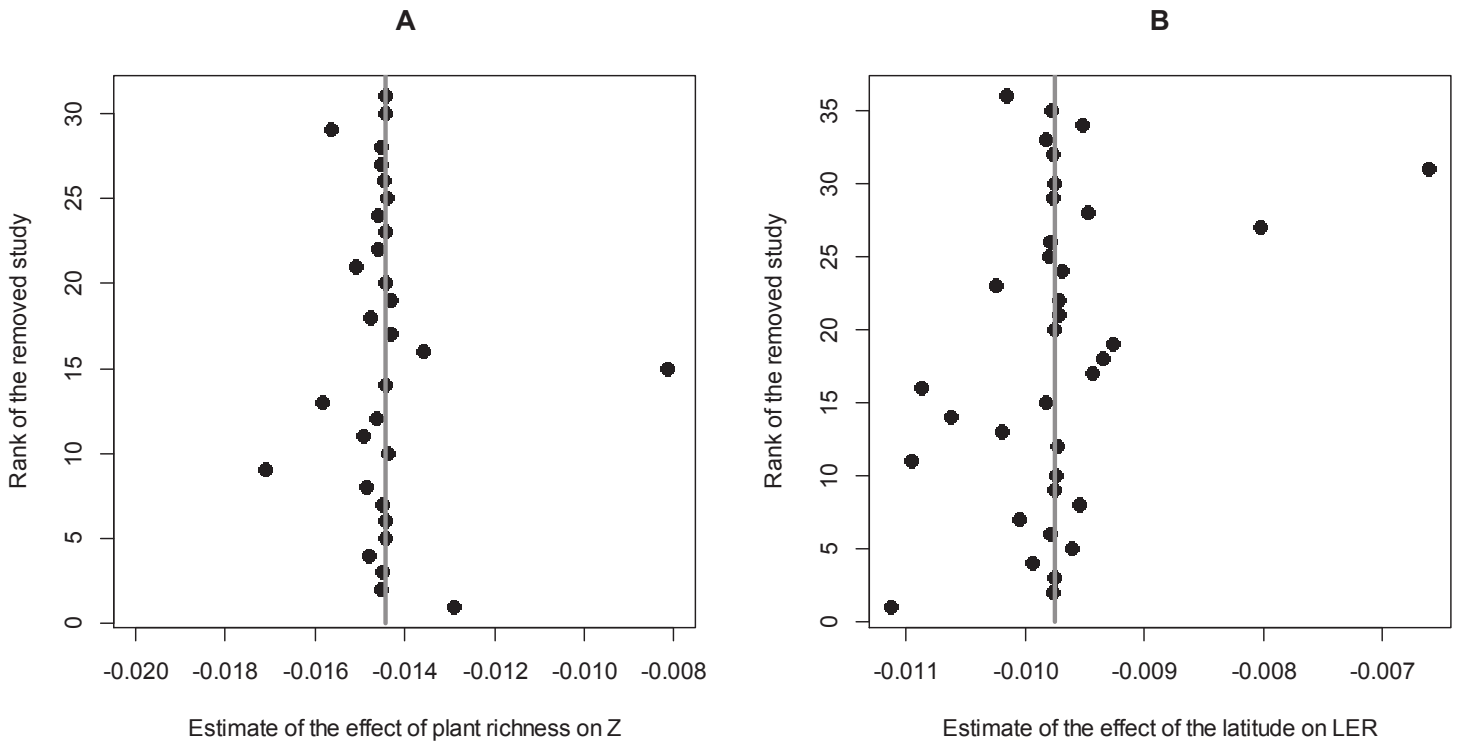

Figure 5. *Sensitivity analysis of the estimate of the plant richness on the size effect Z (A) and the latitude on the LER (B) to the removal of one study. The y axis show the rank of the study removed. The vertical line represents the estimate obtained without study removed (see Table 3 for details on the models without removal).*

4. Discussion

Across the 66 papers analyzed, plant richness tended to have a positive effect on plant productivity in both natural and managed ecosystems. The available evidence indicates that plant richness matters more in agricultural ecosystems than in natural ecosystems. The analysis on effect size and LER provides a general perspective on the most promising grade of plant richness to be used in agricultural systems. Studies reported LER are studies focusing on intercropping with low plant diversity, effect size is reported for multi-species studies.

4.1 Global effects of plant diversity on plant productivity

In our meta-analysis, we found that plant richness increases the overall ecosystem productivity but that the effect size decreased as the magnitude of plant richness increased. A similar but not statistically significant trend was observed for the LER. In other words, the results suggest that the gain in productivity per unit of diversity added decreases as diversity increases. This finding is varying with those of other meta-analyses perhaps because the other analysis focused on short-term experiments with annual plants (Yu et al. 2015) or on grasslands that lack an upper canopy layer (Cardinale et al. 2007, Li et al. 2014, Craven et al. 2016). Our results differ in the magnitude of plant richness with those of a number of other studies that found a positive relationship between plant richness and (Craine et al. 2003, Bessler et al. 2009, Hector et al. 2011, Byrnes et al. 2014b). In the latter studies, however, there was a tendency for productivity to plateau at higher levels of plant richness. Along with our results, this suggests that productivity is maximized by a relatively low number of plant species and that rare plant species contribute less than expected to productivity, probably because of functional redundancy. Our modelling efforts confirmed that increases in diversity should increase productivity but also highlighted that the gain per unit of diversity added decreases as diversity increases, i.e., that the relationship has a plateau (Turnbull et al. 2013). As noted earlier, our meta-analysis revealed that productivity had a positive response to plant richness. This positive response results was stronger in agricultural systems than in natural systems. This is in line with Barot el al. (2017) that argued that since in agricultural systems are driven by human, it should be possible to maximize the ultimate benefits of mixtures.

4.2 Effect of climate on the response of productivity to plant diversity

We found that LER values decreased with latitude (**Figure 1B**). We suspect that the availability of solar radiation, which decreases with latitude (Budyko 1969), might alter the relationship between plant richness and productivity. The strong solar radiation at lower latitudes might promote complementarity between plant species, while the weaker radiation at higher latitudes might promote competition and thereby dampen the effect of plant richness. These explanations, however, are not consistent with two studies that were performed below 10° latitude and that reported low LER values. One of these studies (Agegnehu et al. 2006) was conducted at a high altitude, however, and therefore had conditions that were more similar to those at higher than at lower latitudes. The other study was conducted under arid climatic conditions (Neto et al. 2012) under which water availability probably limited productivity. Our findings are consistent with the resource availability—competition intensity hypothesis, which predicts that competition increases with productivity. We showed that the LER tends to decrease with scarcity of solar radiation (**Figure 4B.**), we suggest that our findings are opposed to the stress-gradient hypothesis (SGH), which predicts a linear increase in the intensity of facilitation as environmental conditions become increasingly stressful (Bakker et al. 2013). This confirms that the design of plant-diversified systems should take into account the local availability or resources. Our results suggest that for mono-strata systems (mostly cereal, grain, vegetable, and legumes) diversification is more likely to be effective in tropical conditions (**Figure 2.**).

4.3 Effect of canopy structure on response of productivity to plant diversity

We found that the response of productivity to plant richness was affected by the type of plants in the community and the number of strata in the canopy. The effect of plant richness on the productivity, for example, was reduced by the presence of trees in the canopy (**Figure 2D, E, F**). We suspect that trees, by greatly reducing the solar radiation for the lower strata (Parker 1995, Fridley 2003).

Possibly, high variances in some architectural traits could also impact the microclimate in and below the canopy and finally modify the productivity (Barot et al. 2017). However, our complete statistical model predicted that the variability in effect size for systems increases with the level of the plant richness in systems with annuals but is stable in systems with perennials (**Figure 6A**). This suggests that perennial plants may help stabilize the productivity across a broad range of plant richness. Despite there are many studies on the biodiversity and ecosystem functioning, in future meta-analysis, it would be valuable to further evaluate the relationship between productivity stabilization and plant richness.

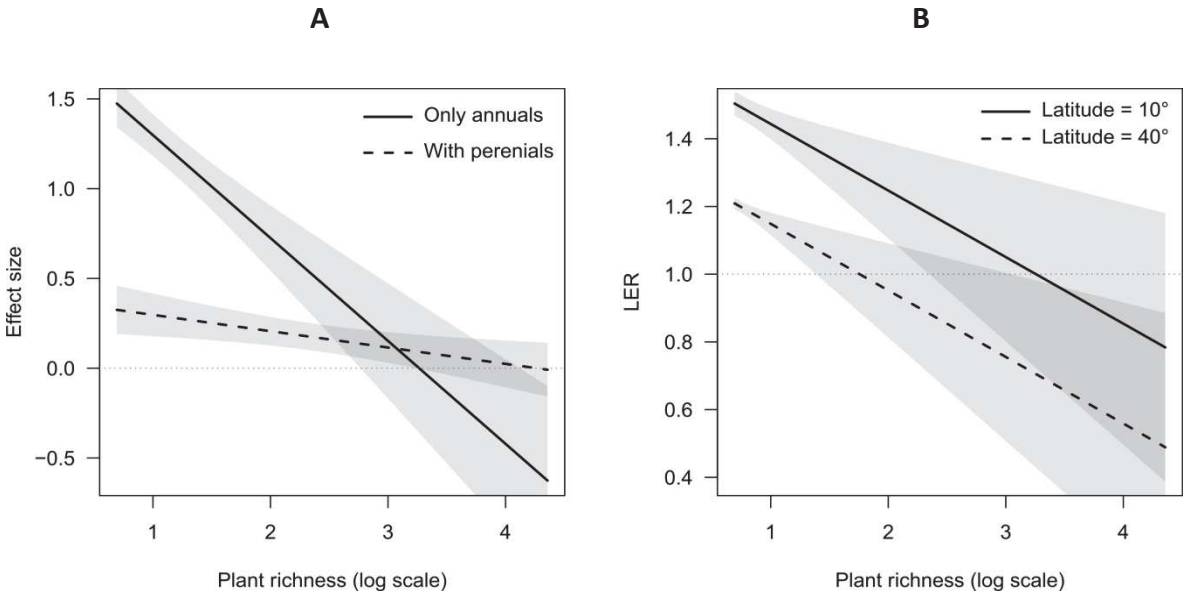

Figure 6. *Prediction of the effect size of plant richness on productivity as a function of the plant richness for systems with only annuals plants or with perennial plants (A), and of the LER as a function of the plant richness for two latitudes (B). The horizontal dotted lines indicate the neutral effect, and the grey areas show the standard error predicted by the models. All statistics of the complete models used for these predictions are presented in Table 3.*

From an agricultural perspective, our results suggest that the intercropping with plant occupying different position in the canopy does not result in systematic overyielding. This is especially likely to be the case for high productivity systems, in which light is often a limiting factor and in which tall plants out compete shorter ones (Rajaniemi 2003). In such systems, different species are more likely to

compete for light than participate in light partitioning. More research is needed to better understand light partitioning between crops because light partitioning is often assumed in the design of intercropping systems (Allen et al. 1976, Ewel 1986).

4.4 Implications for plant diversification of agricultural systems

Agriculture must develop the capacity to moderate the level of diversity in response to yield or harness the ecosystem services provided by biodiversity in terms of sustainable agriculture (Isbell et al. 2015b). There is no absolute answer to the question of how much biodiversity is enough because all systems are dynamic (Main 1999). This means that farmer intervention may be necessary to determine the degree of plant diversity in cropping systems; although simpler agricultural systems are easier to manage.

Intercropping has long been considered a useful approach to the sustainable intensification of agriculture (Bedoussac et al. 2015). On the one hand, we found that most intercropping research has focused on annual plant combinations and has documented that productivity is higher with multiple crops than with monoculture. On the other hand, we found that productivity in multistrata systems was lower than we expected. Additional studies on multistrata intercrops are needed to determine whether they can attain high levels of productivity.

From a practical agricultural perspective, we concluded that moderate plant richness seems sufficient to maximize the productivity. However the provision of other ecosystems services should be considerate. Cardinal et al. (2012a) proposed a framework that links biodiversity to the goods and services provided by ecosystems. Future studies and meta-analyses should determine how plant diversity affects the ability of systems to provide multiple ecosystem services and not simply productivity or yield. The trade-offs among services will not be easy to assess because both the services and the trade-offs occur at very different spatial and temporal scales.

5. Acknowledgments

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Chapter 4 – Effect of plant diversity on the productivity of multi-species tropical agroforestry systems

This chapter is composed of a study that questions how plant diversity affects the crop performance in tropical agroforestry systems. Taking the case of the Talamanca agroforestry systems, we addressed the question: Do more diverse agroforestry systems provide more income to farmers?

The originality of this study was to intend estimating the global production of agroforestry systems. It was particularly interesting to separate the effect of plant diversity for the different functional groups of the plant communities. This helped to better understanding the rules that govern the production in multi-strata systems.

We addressed this question in a broad gradient of systems with 180 plots in 20 farmer fields. The evaluation was as meticulous as possible, with the estimation of the production of each plant in these 180 plots during 1 year. Each individual production was converted into incomes according to local market prices. We analysed the plant diversity – income relation globally (all incomes together) and separately for the incomes generated by each functional group (also corresponding to different strata). This relation was extremely different between functional groups suggesting contrasted complementary/competition for solar radiation according to the strata of the canopy. Complementarity seemed to dominate for plant groups in the upper strata while competition seemed to dominate for plant groups in the lower strata. The detection of complementarity and competition in the different strata enabled us to suggest how management of tropical agroforestry systems can be improved.

This study is currently published in the journal **Agroforestry Systems**.

Effect of plant diversity on income generated by agroforestry systems in Talamanca, Costa Rica

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Keywords: Multi-strata agroforestry systems, productivity, Musa, Cacao, Global evaluation, Economic value

Abstract. Optimal use of resources in agroforestry requires the evaluation of multi-species and multi-strata cropping systems. The current study evaluated the effect of plant diversity on the performance of agroforestry systems in Talamanca, Costa Rica.

Plants in nine 100-m^2 plots in each of 20 fields were classified into five groups (banana, cacao, other fruits, timber, and firewood), and diversity was assessed by the Shannon–Wiener index. The production of each individual plant was estimated and converted into income according to local market prices.

Our results indicated that as plant diversity increased, the income derived per plant increased for other fruits, firewood, and timber and also when all cultivated plants were considered as one group. In contrast, the income derived per plant decreased for banana and cacao as diversity increased.

This suggests that complementarity between plants was stronger than competition for those plants occupying the higher strata of the canopy (i.e., other fruits, firewood, and timber) but that competition was stronger than complementarity for plants occupying the lower strata of the canopy (i.e., banana and cacao). These results increase our understanding of how the composition and the organisation of these agroforestry systems may be optimized.

1. Introduction

Tropical agroforestry systems are often complex associations of multi-functional and uneven-aged trees and crops (Sanchez 1995). Such systems also have a complex spatial and temporal structure (Bhagwat et al. 2008) and are frequently presented as a sustainable alternative to modern intensive agricultural systems (Leakey et al. 2005, Ngo Bieng et al. 2013).

Many people in developing tropical countries depend on agroforestry systems for subsistence, economic income, and other services (Malézieux et al. 2009, Cerda et al. 2014, Paul et al. 2015). In addition to generating timber and firewood, agroforestry can also provide supplementary income from associated tree crops (Nair 2007). In many systems, however, the economic productivity, efficiency, and profitability of agroforestry farms have not been determined, i.e., there is need to quantify the costs and benefits of agroforestry farms in order to justify their propagation and adoption (Molua 2003). From both private and social perspectives, the economic potential of agroforestry farms has not been well studied (Franzel and Scherr 2002, Molua 2003, Rasul and Thapa 2006). The combined productivity and profitability of all cultivated plants in the system, i.e., have scarcely been addressed in complex agroforestry systems. This led us to determine whether farmers derive more income from complex than from simple agroforestry systems. The evaluation of multi-species and multiple-strata cropping systems remains a major challenge (Lamanda et al. 2012).

The practice of agroforestry, i.e., of growing trees and crops together, is frequently promoted based on the idea that trees benefit crops; otherwise, farmers would probably not include the trees (Vandermeer et al. 2002). Species richness and vegetation structure are key components of structural complexity and form the basis of biodiversity (Hooper et al., 2005b). Biodiversity increases he efficient use of resources and promotes positive interaction between species and other ecosystem processes (Tilman and Pacala 1993, Hooper et al. 2005, Nakamura 2008, Smith et al. 2008, Cardinale et al. 2012b). According to Lehman and Tilman (2000) and de Aguiar et al. (2013), diversity increases community productivity but may reduce the productivity of individual species. The negative

effects of competition, which can lead to lower productivity in some species, are offset by complementarity and facilitation between other species, enabling greater productivity at the community level, i.e., greater global productivity.

The Talamanca region in Costa Rica is characterized by highly diversified cropping systems. The natural environment of the Talamanca region has been an inherent part of the life of the indigenous Bribris and Cabecares (Boza 2014). In this region, agroforestry systems tend to mimic the forest both in structure and in species. The association of species follows ancestral rules linked to their functional role (Borge and Castillo 1997). The variability in the composition and structure of the agroforestry systems, however, have been poorly described, and their relevance to ecosystem performance has been little investigated (Deheuvels et al. 2012). The evaluation of the global productivity in these systems is challenging because of the diversity of the plants that are grown.

The agroforestry systems in the Talamanca region include cacao (*Theobroma cacao L.*) and organic banana (*Musa* spp. AAA). Cacao is usually grown with other fruit trees and with shade trees, such as laurel (*Cordia alliodora* Ruiz and Pav.) or cedar (*Cedrela odorata* L.). These shade trees represent species from the natural forest and are either planted or are naturally growing remnants. Banana is an important crop for farmers and is grown with citrus (*Citrus* spp.), avocado (*Persea americana* Mill.), peach palm (*Bactris gasipaes* Kunth), and other fruit trees. Farmers claim that these other fruit trees grow well with cacao and banana (Farmers' personal communication). Other species, such as jicaro (*Crescentia cujete* L.) and senko (*Carludovica palmata* Ruiz and Pav.), are used for crafts, while guava (*Inga* sp.) and turkey tail (*Cupania cinerea* Poepp.) are used for firewood.

In this study, we estimated the productivity and associated income of all plants cultivated in nine 100-m² plots in each of 20 agroforestry fields in the Talamanca region. We provide the first assessment of the global income generated by these systems. We also investigated how the cultivated plant diversity affects the global income and per type of plant.

2. Methods

2.1 Experimental site

This research was performed within the Bribri indigenous territory of Talamanca in Limón Province, south-eastern Costa Rica (9°00′–9°50′ N, 82°35′–83°05′ W). In this region, most people obtain their livelihood from agriculture. The average annual precipitation is 3570 mm, and the average annual temperature is 25.9˚C. The climate is classified as tropical rain forest (bh-T) (Holdrige 1978).

2.2 Data collection

We studied a network of 20 agroforestry fields that included a wide range of diversity and spatial organization. Each field was 900 m^2 (30 m x 30 m). The fields were in four villages (Amubri, Dururpe, Katsi, and Watsi) and were located 200-400 m a.s.l. The farms were selected according to the following criteria: (i) the farmer was available and willing to participate in the research, (ii) the farm area was relatively flat, and (iii) the farm had the potential to produce at least one commercial crop. Each field was divided into nine plots (10 m X 10 m), and plot was the statistical unit used in the rest of the study.

We identified and determined the coordinates for all of the cultivated plants (with a commercial value) in all plots. Each plant was tagged, allowing multiple measures over time. Overall, our dataset included 2299 plants. Herbaceous plants were not recorded.

2.3 Global productivity

To estimate banana yield, we measured the circumference of the pseudostem of the mother plant (1 m above ground level) and the heights of the sucker plants. Using allometric relationships, we estimated the potential production of banana and vegetative tissue for each banana plant (Fernándes and García 1972). In addition, we measured the weight of available bunches and counted the fruits.

Every banana stem was followed during 1 year to precisely measure those that were harvested or lost when plants were pruned or toppled-over.

To estimate cacao yield, we counted healthy cacao pods during the peak harvests in May and November. According to Braudeau cited by (Deheuvels et al. 2012), each pod produces an average of 185 grams of fresh cacao beans. We multiplied this estimate of bean fresh weight by 0.56 to estimate the dry cacao commercial yield.

For every timber tree, total height, commercial height, and DBH (diameter at breast height) were measured with a hypsometer and a diametric tape. Cubic meters of wood were calculated based on empirical relationships reported by Almendarez et al. (2013) and with a form factor of 0.7 for timber species. With firewood species, we applied the same method using a form factor of 0.5.

Production of fruits other than banana and cacao was estimated for each tree using theoretical values reported by another study in the same region (Burgos et al. 2008).

We estimated the incomes generated by each category of plant according to local market surveys of product prices provided by an association of smallholder farmers from Talamanca (APPTA); the estimates were converted into US dollars. Costs of labour, crop management, and land use were not included in our analysis. The market price of the products considered in our study were: banana \$0.14/kg, cacao \$2.25 kg, timber \$0.18/m^3 (regardless of species), firewood \$0.03/m^3, and other fruits between \$0.18 and \$1.80/kg depending on the species.

2.4 Plant diversity

Cultivated plant diversity in each plot was calculated using the Shannon–Wiener index, (Shannon 1948), which was calculated with the 'diversity' function of the 'vegan' package, version 2.2-1 (Oksanen et al. 2015).

We also assigned each plant to one of five categories: (i) banana, (ii) cacao, (iii) other fruit trees, (iv) timber, and (v) firewood. Cacao and banana are mainly sold

for the international market, while other fruit, timber, and firewood are sold locally or used for self-consumption.

Table 1. Names and abundances of the plants in the 20 agroforestry fields studied in Talamanca Costa Rica. The plants were assigned to five categories or groups. Abundance refers to the number of plants in all 20 fields.

Group / Taxa	Abundance
Cacao group	
Hybrid	750
Banana group	
Cavendish AAA	340
Grosmichel AAA	277
Lacatan AA	158
Musa spp. AAA	248
Musa spp. AAB	92
Fruits group	
Citrus × sinensis	38
Citrus x paradisi	1
Citrus × tangerina	5
Citrus x aurantifolia	3
Citrus × limonia	2
Bactris gasipaes	32
Persea americana	19
Crescentia cujete	10
Nephelium mutabile	8
Artocarpus communis	7
Averrhoa carambola	5
Licania platypus	5
Eugenia malaccensis	3
Eugenia stipitata	3
Cocos nucifera	2
Annona purpurea	1
Annona muricata	1
Mangifera indica	1
Carica papaya	1
Morinda citrifolia	1
Bixa orellana	1

Group / Taxa	Abundance
Timber group	
Cordia alliodora	178
Cedrela odorata	15
Dipteryx panamensis	3
Hyeronima alchorneoides	1
Chloroleucon eurycyclum	3
Gliricidia sepium	2
Brosimum alicastrum	1
Diphysa americana	1
Enterolobium cyclocarpum	1
Brosimum lactensis	2
Firewood group	
Cupania cinerea	24
Inga edulis	19
Cecropia obtusifolia	2
Erythrina costaricensis	1
Cordia panamensis	8
Palicourea tetragona	2
Croton billbergianus	3
Neea psychotrioides	3
Naucleopsis naga	1
Trichospermum grewiifolium	1
Cordia lucidula	3
Bursera simaruba	2
Miconia trinerve	1
Spondias mombin	2
Cestrum schlechtendalii	1
Alchornea costaricensis	1
Ocotea mollifolia	1

2.5 Statistical analyses

Generalized linear mixed-effects models (Bolker et al. 2009) [79]were used to examine the relationship between the income generated by each group cultivated plants and plant diversity in each of the 180 plots. We considered the field as a random effect. To analyse the effect of plant diversity on each group, income was expressed per plant to remove the effect of density. Income was considered globally when considered at plot scale. The GLMMs were fitted by the Laplace approximation using the 'lmer' function in the 'lme4' package (Bates et al. 2011). All statistical analyses were performed with R 3.3.1 (R Core Team 2016) and with an alpha level of 0.05.

3. Results

3.1 Cultivated plant diversity

Based on plant composition and spatial structure, the fields ranged from the relatively specialized (e.g., field 6 and 14) to the very complex (e.g., field 16 and 17) (**Figure 1**). We identified 56 taxa (species and varieties) of cultivated plants in the 20 fields (**Table 1**). The timber category included 11 species; *Cordia alliodora* Ruiz and Pav was the most abundant, representing 84% of the individuals. *Cedrela odorata* L., *Dipteryx panamensis*, and *Chloroleucon eurycyclum* were much less abundant species in the timber category. *Cupania cinerea* Poepp. and *Inga edulis* represented 56% of the 18 firewood species. Fruits other than banana or cacao was the most diverse group with 22 taxa; *Citrus x sinensis*, *Bactris gasipaes* Kunth, and *Persea americana* Mill represented 26, 21, and 13%, respectively, of the trees in this category. *Annona muricata*, *Morinda citrifolia*, and *Carica papaya* were also in the other fruits category but were represented by only one individual on specific farms. Cacao (*Theobroma cacao* L.) trees were all hybrids belonging to the Trinitarian variety. We identified eight varieties of banana *Musa* spp., and these were from the AA, AAA, AAB, and ABB groups.

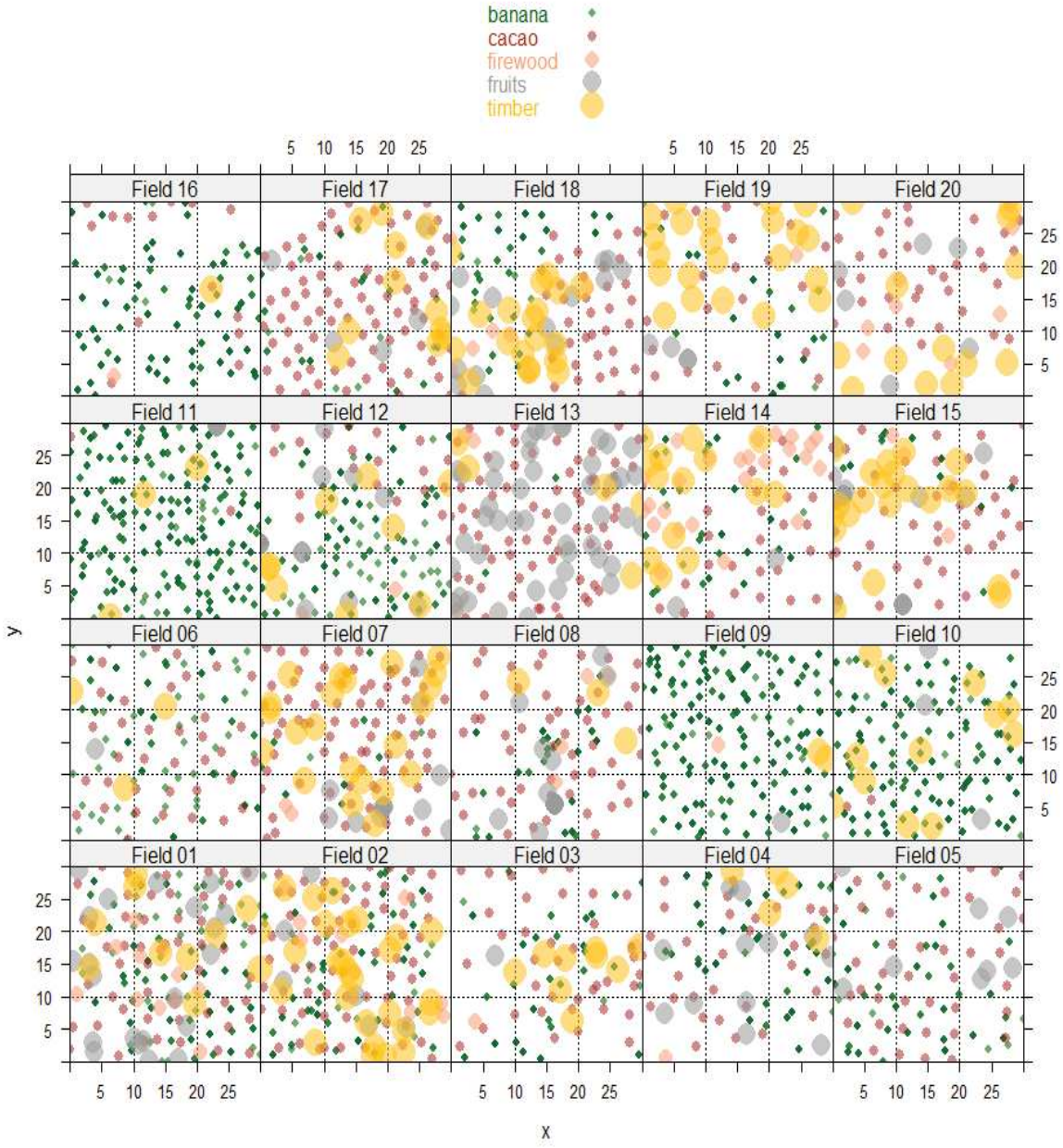

Figure 1. *The diversity and spatial distribution of individual cultivated plants in 20 agroforestry fields in Talamanca, Costa Rica. Each plant was assigned to one of the five categories indicated at the top. The X and Y coordinates are in meters. Plots within fields are delineated by dotted lines.*

Income generated per plant was highest for the other fruits group, followed by the banana, cacao, and timber groups, which had similar incomes (**Figure 2**). Income generated was much lower for the firewood group than for the other four groups. Annually, the average production was 7351 $Kg.ha^{-1}$ kg for banana, 191 $Kg.ha^{-1}$ for cacao, 26 $m^3\ ha^{-1}$ for timber, and 5.25 $m^3\ ha^{-1}$ for firewood.

Cultivated plant diversity had a significant effect on the income generated per plant in each category. As diversity increased, income per plant decreased for banana and cacao but increased for other fruits, timber, and firewood, and also increased when all cultivated plants were considered as one group, i.e., global income increased with diversity (**Table 2, Figure 3**).

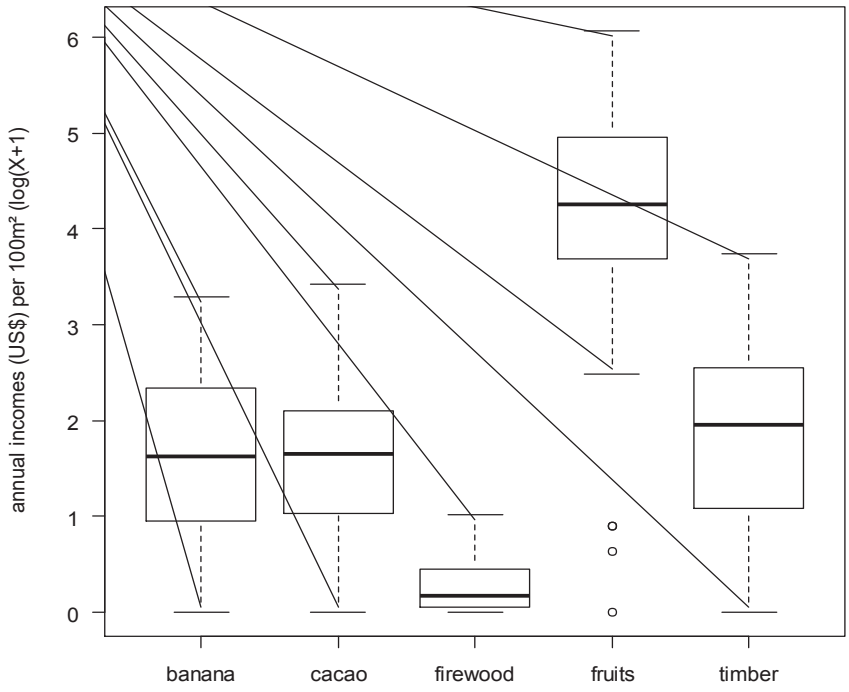

Figure 2. *Estimated mean incomes (log transformed) for each plant group summed in each of the 180 plots in 20 agroforestry fields in Talamanca, Costa Rica.*

Table 2. Relationship between income generated per plant (in each of five categories plus all categories of plants) and plant diversity in 180 plots in 20 agroforestry fields in Talamanca Costa Rica. A generalized linear model including field as a random effect was used for the analysis. The significance of plant diversity was tested against the null model. Note that increases in diversity decreased income per plant for banana and cacao but increased income per plant for the other categories.

Response variable	Df	Estimate	AIC	ΔAIC	log-Likelihood	Chi-sq	P
All plants	3	66.61	2059.35	20.48	-1026.67	22.48	<0.0001
banana	3	-0.12	10.01	5.25	-2.01	7.25	0.0071
cacao	3	-0.23	240.90	5.03	-117.45	7.03	0.0080
fruits	3	3.70	1197.72	7.15	-595.86	9.15	0.0025
firewood	3	0.01	-753.33	2.50	379.67	4.50	0.0340
timber	3	0.26	288.56	5.30	-141.28	7.30	0.0069

Df: degrees of freedom, AIC: Akaike information criterion, ΔAIC: difference of AIC with the null model, Chi-sq: value of the Chi-square test, P: P-value of the Chi-square test.

4. Discussion

4.1 Cultivated plant diversity

The 180 agroforestry plots in Talamanca, Costa Rica, exhibited a large range of plant diversity (the Shannon–Wiener index ranged from 0 to > 2), and the high diversity in some of these fields confirmed previous reports (Kapp 1989, Borge and Castillo 1997, Guiracocha 2000, Deheuvels et al. 2012). Plant density and spatial organization (**Figure 1**) suggested that farmers consider banana and cacao as the primary crops and timber and other fruits as secondary or complementary crops.

As pointed out by the farmers interviewed, these complex cultivated plant communities reflect two main management strategies: i) to establish cacao and

banana in remnant forests and ii) to establish other fruits during the natural regeneration of timber and firewood trees. Trees from natural regeneration are usually preferred because they do not have to be purchased. In addition, regenerated trees are generally thought to be better adapted than planted trees to site conditions (de Sousa et al. 2016). The range in species diversity observed in this study was similar to that observed in previous studies (Anglaaere et al. 2011, Deheuvels et al. 2012, Ngo Bieng et al. 2013).

4.2 Global productivity

Banana was the most abundant group with an average population density of 1100 plants ha^{-1}, which is not very different from the population density in intensively managed commercial plantations (1600 to 1900 plants ha^{-1}). This highlights the importance of banana to the agroforestry farmers in Talamanca, Costa Rica.

The average productivity of cacao was 191 $Kg.ha^{-1}$ $year^{-1}$, which was somewhat higher than the 136 $Kg.ha^{-1}$ $year^{-1}$ reported by Deheuvels et al. (2012) for similar agroforestry systems in Talamanca. Such yields are substantially lower than those of cacao agroforestry systems in Ghana and Ivory Coast, which average 456 and 214 $Kg.ha^{-1}$ $year^{-1}$, respectively (Gockowski and Sonwa 2011). As noted by Deheuvels et al. (2012), the low cacao yields in Talamanca result from the absence of chemical input and from losses caused by the fungus *Moniliophtora roreri*, the agent of cacao frosty pod rot disease.

The average *C. alliadora* timber production in the current study (26 m^3 ha^{-1}) was substantially lower than the 48 m^3 ha^{-1} recently reported for Central America (Somarriba et al. 2014). This may result from differences in sites and planting densities. Although the yields in the current study are low, they clearly represent a key economical input for smallholders, especially when cacao prices are low (Ramírez et al. 2001). Relative to timber, firewood is not a key economic input and averaged 43 trees ha^{-1}, which corresponds to 5.25 m^3 ha^{-1}. According to the farmers interviewed, these species are not sold but are used by the farmers themselves.

The evaluation of the productivity of other fruits trees was difficult because of their seasonal variation. Our estimation of income from these fruits tree is clearly

higher than other cultivated plants (**Figure 2**). Although farmers don't have production records, this result is consistent with farmer's perception since they claim good yielding for fruit trees.

4.3 Relationships between income and plant diversity

Our results indicate that the effect of plant diversity on income depended on the plant group producing the income (**Figure 3**). Income generated by higher strata plant groups (other fruit trees, timber, and firewood) were positively correlated with plant diversity, while income generated by lower strata plant groups (banana and cacao) were negatively correlated with plant diversity. These results suggest that complementarity rather than competition dominated for the higher strata plants. Similar results have been reported in tropical and temperate forests (Hooper et al. 2005, Zhang et al. 2012, Jucker et al. 2014). In contrast, competition rather than complementarity apparently dominated for the lower strata cultivated plants. We suspect that the negative relationship between income generated by banana and cacao and plant diversity mainly resulted from competition for light.

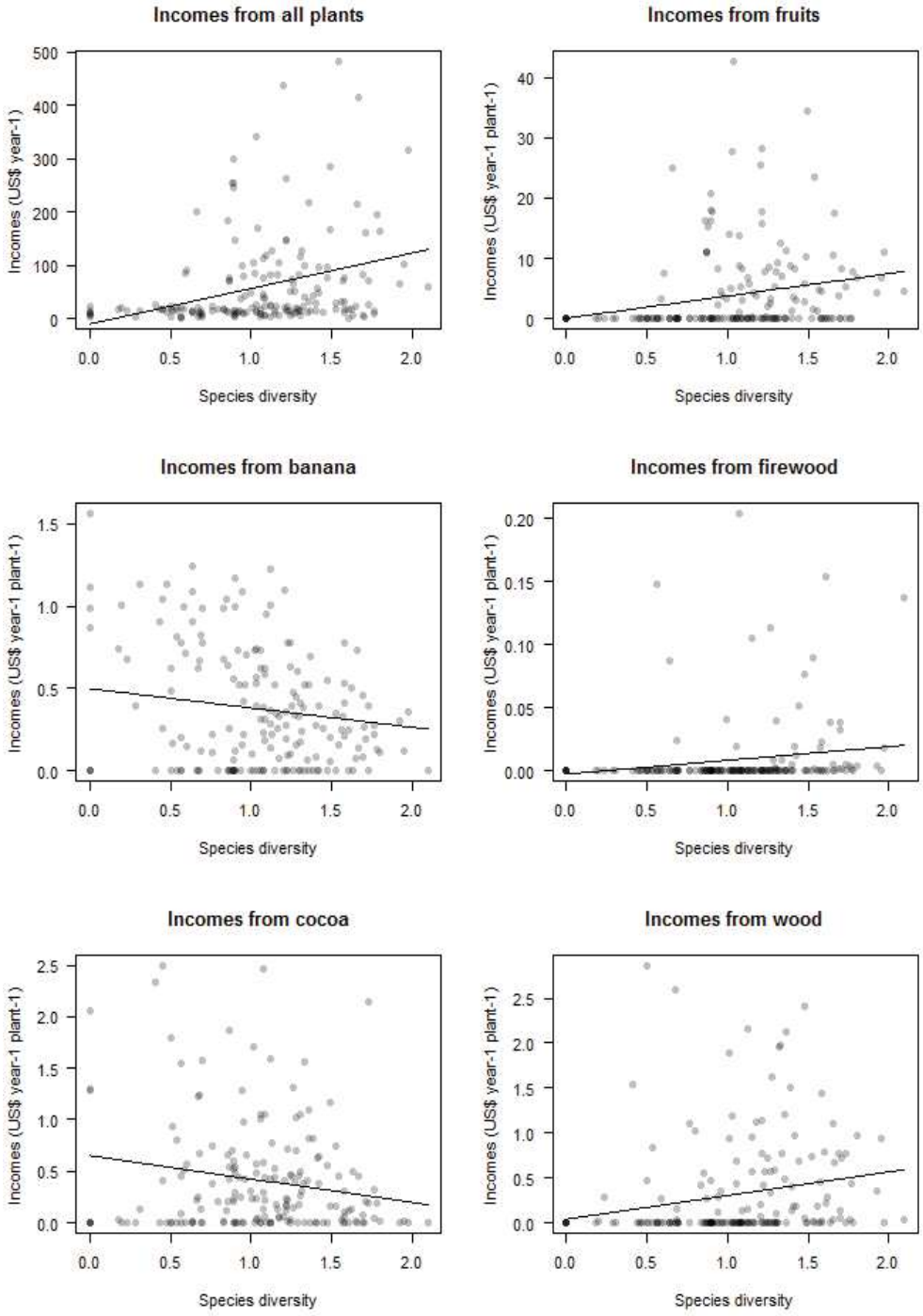

Figure 3. *Total mean income for all plants (global income) and in each group in response to plant species diversity in 20 agroforestry fields in Talamanca, Costa Rica. Diversity was assessed using the Shannon–Wiener index. Each circle indicates the mean value from one of the 180 plots. The lines show the prediction of the generalized linear model that included field as a random effect.*

For the higher strata, our results are in-line with other studies that showed that functional complementary or facilitation may occur in complex plant communities (Hooper and Vitousek 1997, Smith et al. 2008, de Aguiar et al. 2013, Franco et al. 2015). As noted, however, the effect of diversity became negative at a lower canopy level in the current study. This suggests that when light becomes scarce, complementarity is reduced. This hypothesis is consistent with previous studies that found that overyielding is reduced when the availability of an essential resource (mineral nitrogen in soil) decreases (Reich et al. 2003, Dybzinski et al. 2008, Lebauer and Treseder 2008, Jarchow and Liebman 2012). Our result is inconsistent with the gradient stress hypothesis, which predicts that interactions among plants shift from facilitation to competition as environmental stress decreases (Maestre et al. 2009). When all cultivated plants were treated as one group in the current study, the income per plant was positively related to plant diversity. This positive relationship was largely explained by the other fruits group, whose positive relationship with diversity more than countered the negative relationships for banana and cacao. Although we tried our best to assess the real value of other fruits, we may have slightly overestimated the value because some fruits are consumed by the grower and are not sold. This study suggests that an increase in the density of other fruit trees and therefore in fruit production could increase farmer income, but this possibility is limited by the poor access to markets in the region. Extension services and government incentives should probably focus on organizing distribution channels to facilitate the sale of fruit produced from these systems.

Our results show that the effect of diversification on farmer income reflects a close balance between complementarity and competition. The results also suggest that complementarity might be increased by increasing plant diversity within the same stratum of the canopy. This could lead to some specialisation within fields such that banana are grown in one part of the field and other trees are grown in other parts.

5. Acknowledgments

We thank the farmers who allowed us to use their farms for this study; Alonso Porras, Bruno Lopez, Federico Gomez, and Marvin Lizano for assistance with data collection; and Walter Rodriguez from APPTA for technical information.This study received financial support from the Instituto Tecnológico de Costa Rica and Instituto Francés de América Central. This work is part of the Scientific Partnership Platform on Agroforestry Systems with Perennial Crop (PCP AFS-CP) led by CIRAD and CATIE. Finally, we thank Bruno Rapidel (CIRAD) for his comments on an early version of this manuscript.

Chapter 5 – Modelling and design of multi-species cropping systems, case of agroforestry systems

This chapter is complementary to the Chapter 4; it addresses specifically how the structure of the plant community affects productivity of crops in complex agroforestry systems. Here, the focus was made on the production of banana plants and cacao tree according to the composition of their neighbourhood.

To improve the management of diversified cropping systems is crucial to understand how plants interact in spatially heterogeneous communities. However, in such complex systems, methods to disentangling these interactions are lacking, because each plant is embedded in a unique assemblage of associated plants, i.e., in a unique "neighbourhood", and process-based models are difficult to parameterize. Here, we present an original individual-based statistical approach that allows the assessment of interactions in highly complex agroforestry systems. We applied our methodology in 19 plots (1 plot is missing, because the absent of banana plants) in farmer fields in Talamanca, Costa Rica to analyse the production of banana and cacao. One strength of our method is that we did not choose on *a priori* distance assumptions regarding of effect between plants. Our results highlight how yield can be improved in these systems and allow us to discuss the characterization of competition/facilitation processes concern to specific tropical systems. However, the individual-based approach used should be applicable to other complex plant communities.

This study is currently submitted in the journal **European Journal of Agronomy.**

Individual-based analysis of interactions between plants: a statistical modelling approach applied to banana and cacao in heterogeneous multistrata agroecosystems

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Keywords: potential yield; spatial structure; neighboring plant; productivity; agroforestry, Costa Rica.

Abstract. Understanding how the spatial organization of diversified plant communities alters their performance is an important step in designing and managing diversified agroecosystems. The high level of spatial heterogeneity in tropical agroforests makes this task challenging. In 19 agroforestry plots in Talamanca (Costa Rica), we analyzed the effect of the structure of the plant community in the neighborhood of each individual cacao tree and banana plant on their yield. We developed an individual-based analysis in two steps. First, we selected without *a priori* assumptions on the distance at which the number of neighboring plants of a given functional group (banana plants, cacao trees, fruit trees, or wood trees) best explained the proportion of potential yield (PPY) of cacao and banana plants. In a second step, we tested the significance of the abundances of the four groups of plants in a complete model that predicted the PPY of banana and cacao plants. The abundance of neighboring plants did not increase banana PPY expect in the case of other banana plants, suggesting that banana plants yield better when aggregated. All other groups of plants reduced both banana and cacao PPY, except that the effects of wood trees were not significant. The optimal plant densities suggested by our analysis are similar to those recommended in monoculture. The two complete linear models predicted about 60% of the variance of the average response of the PPY to the neighboring plant assemblage. Our results also suggest that banana productivity may be increased by growing bananas in association with trees, especially with cacao trees and with moderate densities of larger trees.

1. Introduction

Researchers are increasingly studying tropical agroforests as models for sustainable agricultural (Sperber et al. 2004, Leakey et al. 2005, Tscharntke et al. 2011). Tropical agroforests are characterized by associations of multi-strata, multi-functional, and uneven-aged trees and crops, resulting in high species richness and high structural complexity of the vegetation (Sanchez 1995, Ngo Bieng et al. 2013). Few authors have tried to link the structural complexity of different land uses to productivity (Steffan-Dewenter et al. 2007). Understanding how the spatial organization of plants affects productivity is important for improving the design and management of complex systems (Baskent and Jordan 1996). However, the substantial spatial heterogeneity of highly diversified systems makes this task challenging. In such complex systems, each plant has a unique "neighborhood", making the establishment of generic rules at the field scale extremely difficult.

In the Talamanca region of Costa Rica, researchers have described how agroforests provide ecosystem services (such as carbon sequestration and biodiversity conservation) but have paid far less attention to how the overall productivity of such forests is related to their structure (Somarriba and Harvey 2003, Suatunce et al. 2003). These descriptive studies led the authors to suggest that improvements in crop management, including improvements in spatial structure, are needed to increase productivity. The evaluation of productivity in the agroforestry systems in the Talamanca is challenging because of the diversity of the plants that are grown. These systems can include from one to more than 30 associated tree species (Guiracocha et al. 2001). Two important cash crops in this region are cacao (*Theobroma cacao* L.) and organic banana (*Musa* spp.), which are perennial and semi-perennial, respectively. In addition to often being grown together, cacao and banana are usually grown with other fruit trees such as citrus (*Citrus* spp.), avocado (*Persea americana* Mill.), and peach palm (*Bactris gasipaes* Kunth), and also with shade trees, such as laurel (*Cordia alliodora* Ruiz and Pav.) or cedar (*Cedrela odorata* L.). These shade trees

represent species from the natural forest and are either planted or are naturally growing remnants.

Even when a field is composed of plants of the same species, the processes that determine how individual plants compete for resources are complex, because plants are forced to share limited resources (Sinoquet and Cruz 1995). The spatial organization of individuals in a community may be one of the most important structural characteristics that influence complementarity between species, biodiversity, and ecosystem functioning (Mokany et al. 2008, Perfecto and Vandermeer 2008, Pringle et al. 2010). Few studies of vegetation structure in agroforests, however, have dealt with spatial structure, i.e., the horizontal organization of individuals in space and the relationships between individuals in a "neighborhood" (Illian et al. 2008, Ngo Bieng et al. 2011). Although spatial heterogeneity of plants is recognized as a powerful promoter of coexistence between plants (Monzeglio and Stoll 2005), explaining species performances remains challenging in fields where plant spatial organization is heterogeneous. In such fields, an individual-based analysis (i.e., an analysis of individual plants, their properties, and their surroundings) may be useful (DeAngelis and Grimm 2014).

In this paper, we analyzed how the structure of the plant community in the neighborhood of individual cacao and banana trees affects their yield (assessed by the proportion of potential yield, PPY). We used a data set of 19 plots of agroforestry systems in Talamanca, Costa Rica. The analyses had two steps. First, we determined the area around each banana plant or cacao tree (as indicated by a radius) in which the number of trees of a given neighboring group (including banana plants, cacao trees, fruit trees, or wood trees) best explained the PPY of cacao and banana. Second, we tested the significance of the abundance of the four groups of plants in a complete model that predicted the PPY of banana and cacao plants. Based on the results, we finally discuss how the production of banana and cacao can be optimized in complex, multistrata agroecosystems.

2. Methods

2.1 Field sites

This research was performed in the Bribri indigenous territory of Talamanca, Limón Province, south-eastern Costa Rica (9°00′–9°50′ N, 82°35′–83°05′ W). The average annual precipitation is 3570 mm, and the average annual temperature is 25.9˚C. The climate is classified as tropical rain forest (bh-T) (Holdrige 1978). The studied sites contain typical agroforestry systems in which the principal commercial crops, banana and cacao, are accompanied by a wide range of other tree species. The selected fields have diverse spatial arrangements with densities of banana ranging from 22 to 1778 plants per ha and those of cacao ranging from 0 to 900 plants per ha (see **Figure 1** for maps of plots).

We studied a network of 19 agroforestry fields; each field was 900 m^2 (30 m x 30 m). The selected cropping systems represent the smallholder farms (2 ha on average) in the Talamanca region, and the species spatial design follows ancestral rules that are linked to the trees' functional roles in natural forests. The productivity of farmers in this region is limited by low levels of education, infrastructure, and community development (Borge and Castillo 1997).

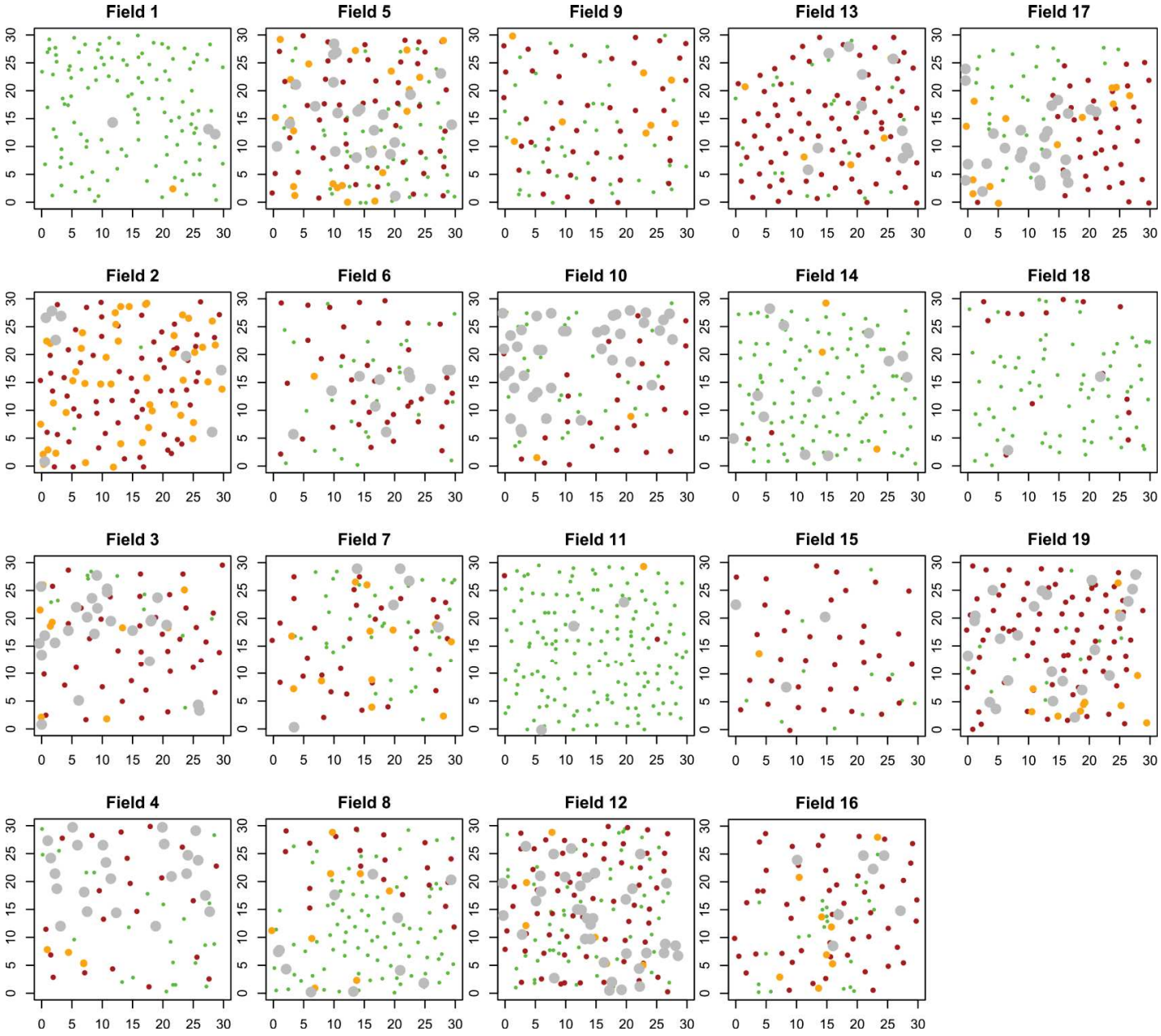

Figure 1. *Maps of the diversity and spatial distribution of individual cultivated plants in the 19 studied plots in Talamanca, Costa Rica. Each plant was assigned to one of the four categories (green: banana plants, brown: cacao trees, orange: fruit trees, grey: wood trees). The X and Y coordinates are in meters.*

Table 1. The plant taxa measured in this study and their assignment to the four functional groups.

Cacao group	**Wood tree group**
Theobroma cacao - Trinitarian	*Cordia alliodora*
Banana group	*Cedrela odorata*
Musa - Cavendish AAA	*Dipteryx panamensis*
Musa - Grosmichel AAA	*Hyeronima alchorneoides*
Musa - Lacatan AA	*Chloroleucon eurycyclum*
Fruits tree group	*Gliricidia sepium*
Citrus × sinensis	*Brosimum alicastrum*
Citrus x paradisi	*Diphysa americana*
Citrus × tangerina	*Enterolobium cyclocarpum*
Citrus x aurantifolia	*Brosimum lactensis*
Citrus × limonia	*Cupania cinerea*
Bactris gasipaes	*Inga edulis*
Persea americana	*Cecropia obtusifolia*
Crescentia cujete	*Erythrina costaricensis*
Nephelium mutabile	*Cordia panamensis*
Artocarpus communis	*Palicourea tetragona*
Averrhoa carambola	*Croton billbergianus*
Licania platypus	*Neea psychotrioides*
Eugenia malaccensis	*Naucleopsis naga*
Eugenia stipitata	*Trichospermum grewiifolium*
Cocos nucifera	*Cordia lucidula*
Annona purpurea	*Bursera simaruba*
Annona muricata	*Miconia trinerve*
Mangifera indica	*Spondias mombin*
Carica papaya	*Cestrum schlechtendalii*
Morinda citrifolia	*Alchornea costaricensis*
Bixa orellana	*Ocotea mollifolia*

2.2 Determination of plant community structure

From February to April 2015, we identified and determined the coordinates for all of the cultivated plants (with a commercial value, we did not accounted for weeds that are regularly control manually all over the fields) in each plot. Plants without commercial value were not included in this study. Plants with commercial value were identified to either the species or family level and were assigned to one of four categories: banana plants, cacao trees, wood trees, and fruits trees. Wood trees include timberwood trees and firewood trees, this group were the tallest, forming the top canopy layer (with a maximum height of 40 m). The intermediate vegetation layers were represented by fruit trees (with a maximum height of 26 m), and cacao and banana were located in the lower strata (with an average height of 6 m). The locations of plants of each category in each plot are shown in Figure S1. Plants shorter than 1.5 m were not recorded. The data set included 2299 plants, and the plant taxa in the data set are listed in **Table 1**.

2.3 Determination of the PPY for banana plants and cacao trees

Our goal was to determine for each banana plant or cacao tree how much of their potential growth or production was achieved. We assumed that the potential growth (banana plants) and potential production (cacao trees) was depending on the size of each plant at the first date of measure. By plotting the growth or the production according to the initial biomass or circumference, we were able to define an envelope curve that we assumed to represent the potential of growth or production of a plant for a given initial size. This potential growth or production represents the maximal values in the conditions of our plot networks. Similar to classical yield gap analyses (Neumann et al. 2010), we selected the shape of the envelop curves according to biological hypotheses with the stop of the growth after flowering for banana plants and a decrease of the production for older cacao trees.

The study included three varieties of banana: Cavendish, Gros Michel, and Lacatan. In April 2015, we used allometric relationships (Fernándes and García 1972, Yamaguchi and Araki 2004, Damour et al. 2012, Ripoche et al. 2012) to estimate banana vegetative dry biomass based on the circumference of the pseudostem of each mother plant (1 m above ground level), following the equation:

Dry Biomass= 0,31287 + 0,09546 * Girth

With the Dry Biomass in Kg and the Girth measured at 1m (in cm).

By measuring the circumferences again in July 2015, we were able to estimate the increase in vegetative biomass during the 17 weeks between measurements. The interval between measurements was identical for all plants. We assumed that the potential growth of banana followed a parabolic curve. In this curve, the decrease in vegetative biomass growth for plants with bigger initial biomass corresponds to the progressive switch of banana from vegetative to reproductive growth (this later was not taken into account in our study). The proportion of potential yield (PPY) for each banana plant was then calculated as the ratio of measured increase in biomass to potential increase in biomass.

We estimated cacao yields by summing the healthy cacao pods counted on each tree during the two peaks of harvests in May and November 2015 (Deheuvels et al. 2012). We determined the potential yield for each tree based on the circumference of the tree at 1 m above ground level in April 2015. Similarly to banana plants, we determined the gap between the observed and potential yield for each cacao tree. We assumed that the potential number of pods depended on the tree girth (measured in April 2015 and assumed not to dramatically change during the year of measures) following a log-normal curve. This type of curve allows taking into account the increase of the yield potential from small to medium size trees and then its decrease for bigger (older) trees. The PPY of cacao tree was then calculated as the ratio between the measured number of pods and the potential number of pods for the same girth.

2.4 Statistical analysis

Our aim was to determine the effect of neighboring plants on the PPY of banana and cacao plants. To this end, we used a linear mixed-effect model with the PPY as a response variable and the number of neighboring plants of each category as predictors. In all cases, the plot was included as a random factor on the intercept of the model, which enabled us to take account for the variability due to the conditions of each plot: pest and diseases, soil, landscape context, and crop management. We carried out the analysis in two steps. First, we determined the

radius that best explained the PPY. We used linear mixed models, with the number of plants of one category at a time (banana, cocoa, wood trees, fruit trees) as a predictor. The log-likelihood of the model was used as an estimator of the goodness of fit (McCullagh 1984). For each category of plants, we selected the radius with the greatest log-likelihood. When more than one peak was observed, we selected the one with the smaller radius because a small radius has a minimal implication in terms of management for farmers (smaller area to consider). In the second step, we tested the significance of the effect of the predictors (number of plants of each category of plants that were within the radius determined in the first step of the analysis) on the PPY in a complete model. We also determined whether the quadratic value of each predictor was significant (significance would indicate a non-linear response to the predictor). All models were fitted with the 'lmer' function in the 'lme4' package (Bates et al. 2011). All statistical analyses were performed with R 3.3.0 (R Core Team 2016) and with an alpha level of 0.05.

3. Results

The patterns of biomass increase plotted on initial circumference were similar for the three varieties of banana (**Figure 2A, B, C**). The vegetative growth of the banana plants increased as their initial biomass increased but then decreased slightly when reproductive growth began. The maximal increase in biomass differed among varieties; at 4 months, when the increase was greatest, the increase was 12, 10, and 9 kg for Gros Michel, Cavendish, and Lacatan varieties, respectively. For cacao most of the trees produced a small number of cacao pods, i.e., between 0-10 pods/tree (**Figure 2D**). Only a few cacao trees produced more than 10 pods. The potential number of pods produced increased as the stem circumference increased up to 13 cm and then decreased.

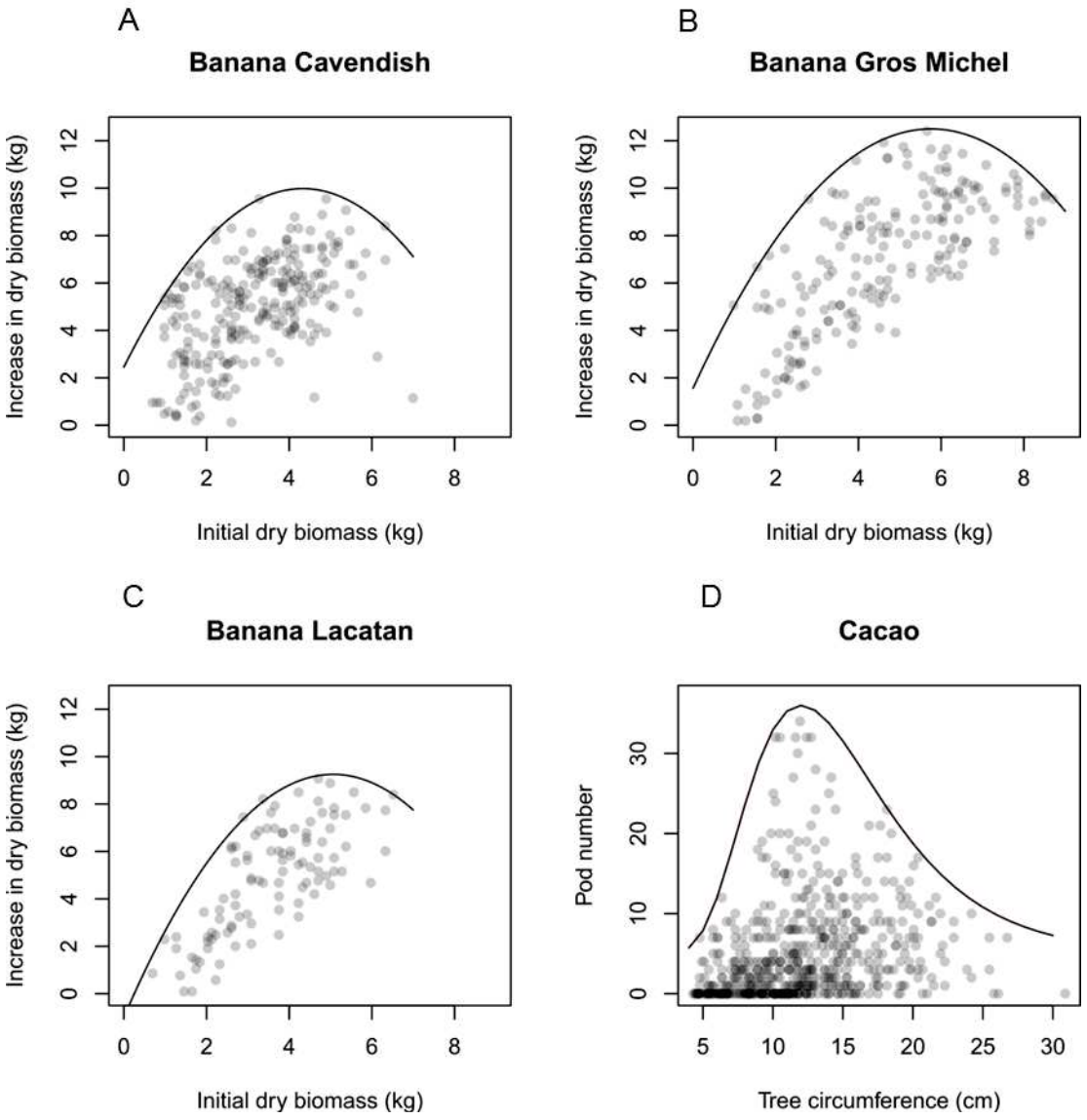

Figure 2. *Relationship between biomass increase and initial plant circumference for the three varieties of banana and between pod number and initial tree circumference for the one variety of cacao. Circumference was measured 1 m above soil level. Each dot represents the data from a single banana plant or cacao tree. The increase in banana biomass was estimated over a 17-week period. Cacao pod numbers are the totals of two harvest periods. For the three banana varieties, the curves show that the vegetative growth rate increased up to the reproductive stage and then slightly declined. For cacao, the curve shows that the number of cacao pods increased as the initial tree circumference increased up to 13 cm and then greatly decreased.*

The radii that best predicted banana and cacao PPY based on the abundance of neighboring plants, i.e., banana plants (vb), cacao trees (vc), fruit trees (vf), and wood trees (vt), are presented in **Figures 3** and **4**. The radius that best explained the variability in the PPY of banana plants was 2.6 m for other banana plants, 2.9 m for cacao trees, 6.2 m for fruit trees, and 7.8 m for wood trees (**Figure 3**). The radius that best explained the variability in the PPY of cacao trees was 3.9 for banana plants, 5.5 m for other cacao trees, 3.9 m for fruit trees, and 5.1 m for wood trees (**Figure 4**). After backward selection, three predictors for banana PPY (vb2.6, vc2.9, and vf6.2) and three for cacao PPY (vb3.9, vc5.5, and vf3.9) were significant in a complete model; vt was not significant in either model (**Table 2** and **3**). For the banana PPY model, the quadratic terms of vc and vf were also significant or nearly significant. We graphically verified the normality of the residues of the two complete models (see **Figure S1**).

Table 2. Results of the analysis of deviance on the effect of neighboring plants on the proportion of potential yield (PPY) of banana plants with a mixed-effect linear model (with the plot as a random factor on the intercept).

Predictors	Df	AIC	LRT	P
Vb	1	-80.953	156.298	0.00007
Vc	1	-94.413	21.704	0.14069
vc^2	1	-92.689	38.944	0.04845
vf^2	1	-92.995	35.886	0.05818
vt	1	-94.685	18.984	0.16826

Df: degrees of freedom, AIC: Akaike information criterion, LRT: Likelihood-ratio test, P: p-value of the Chi-square test, vb: number of banana plants within a 2.6-m radius, vc: number of cacao trees within a 2.9-m radius, vf: number of fruit trees within a 6.2-m radius, vt: number of wood trees within a 7.8-m radius.

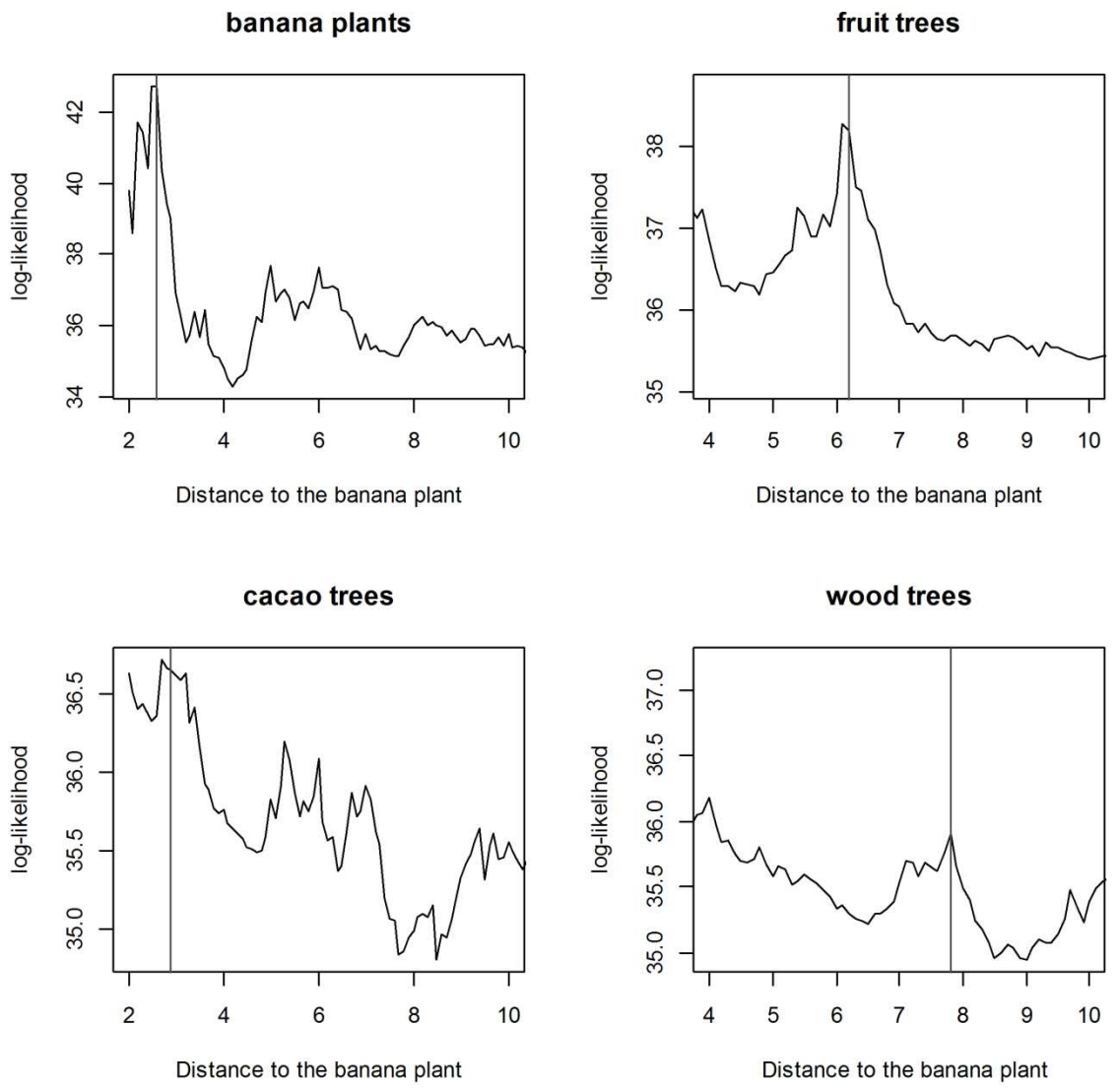

Figure 3. *Selection of the distances (radii) at which each category of neighboring plant had the most effect on the log-likelihoods of the predictions of the proportion of potential yield (PPY) of banana. The distances correspond to the highest differences in AIC values from the null model (AIC). The distance or radius that best predicted the PPY of banana plants was 2.6 m for other banana plants, 2.9 m for cacao trees, 6.2 m for fruit trees, and 7.8 m for wood trees.*

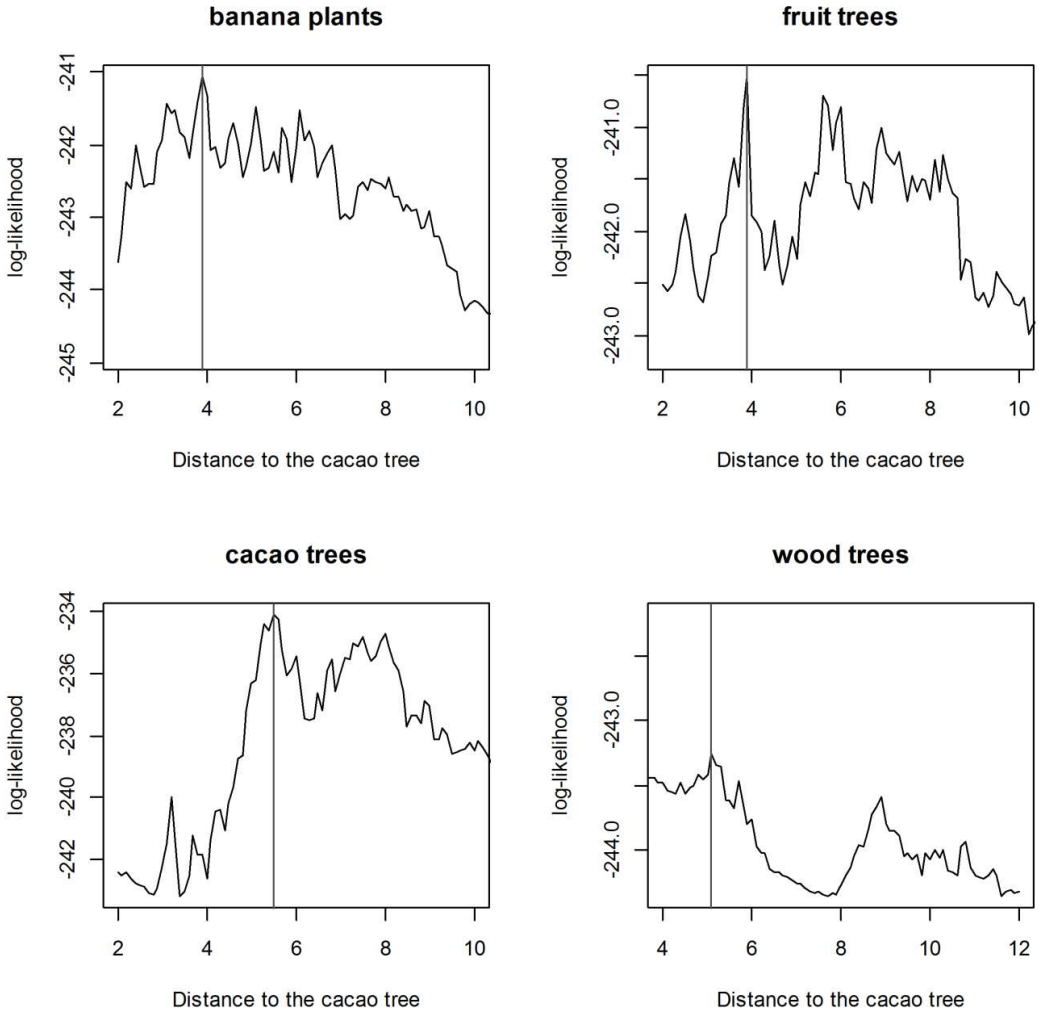

Figure 4. *Selection of the distances (radii) at which each category of neighboring plants had the most effect on the log-likelihoods of the predictions of the proportion of potential yield (PPY) of cacao. The distances correspond to the highest differences in AIC values from the null model (AIC). The distance or radius that best predicted the PPY of cacao trees was 3.9 m for banana plants, 5.5 m for other cacao trees, 3.9 m for fruit trees, and 5.1 m for wood trees.*

Table 3. Results of the analysis of deviance on the effect of neighboring plants on the proportion of potential yield (PPY) of cacao trees with a mixed-effect linear model (with the plot as a random factor on the intercept).

Predictors	Df	AIC	LRT	P
vb	1	461.79	5.9602	0.01463
vc	1	474.66	18.8301	0.00001
vf^2	1	462.44	6.6052	0.01017
vt^2	1	455.89	0.0630	0.80185

Df: degrees of freedom, AIC: Akaike information criterion, LRT: Likelihood-ratio test, P: p-value of the Chi-square test, vb: number of banana plants within a 3.9-m radius, vc: number of cacao trees within a 5.5-m radius, vf: number of fruit trees within a 3.9-m radius, vt: number of wood trees within a 5.1-m radius.

Interestingly, only vb2.6 had a positive effect on banana PPY, and the relationship plateaued above 6 banana plants (**Figure 5**). The other three predictors had a negative effect on banana PPY (**Figure 5**). When the number of cacao trees exceeded 3 within a 2.9-m radius, the banana PPY clearly decreased. The three significant predictors had a negative effect on cacao PPY (**Figure 6**). The negative slope was steepest for the effect of vc.

When the PPY values predicted by the complete model (a model that included all significant predictors; see Table 2 and 3) were plotted on the observed PPY values, the R^2 value was 0.60 for banana and 0.57 for cacao (**Figure 6**). In other words, the models that included the effects of all three categories of neighboring plants performed well.

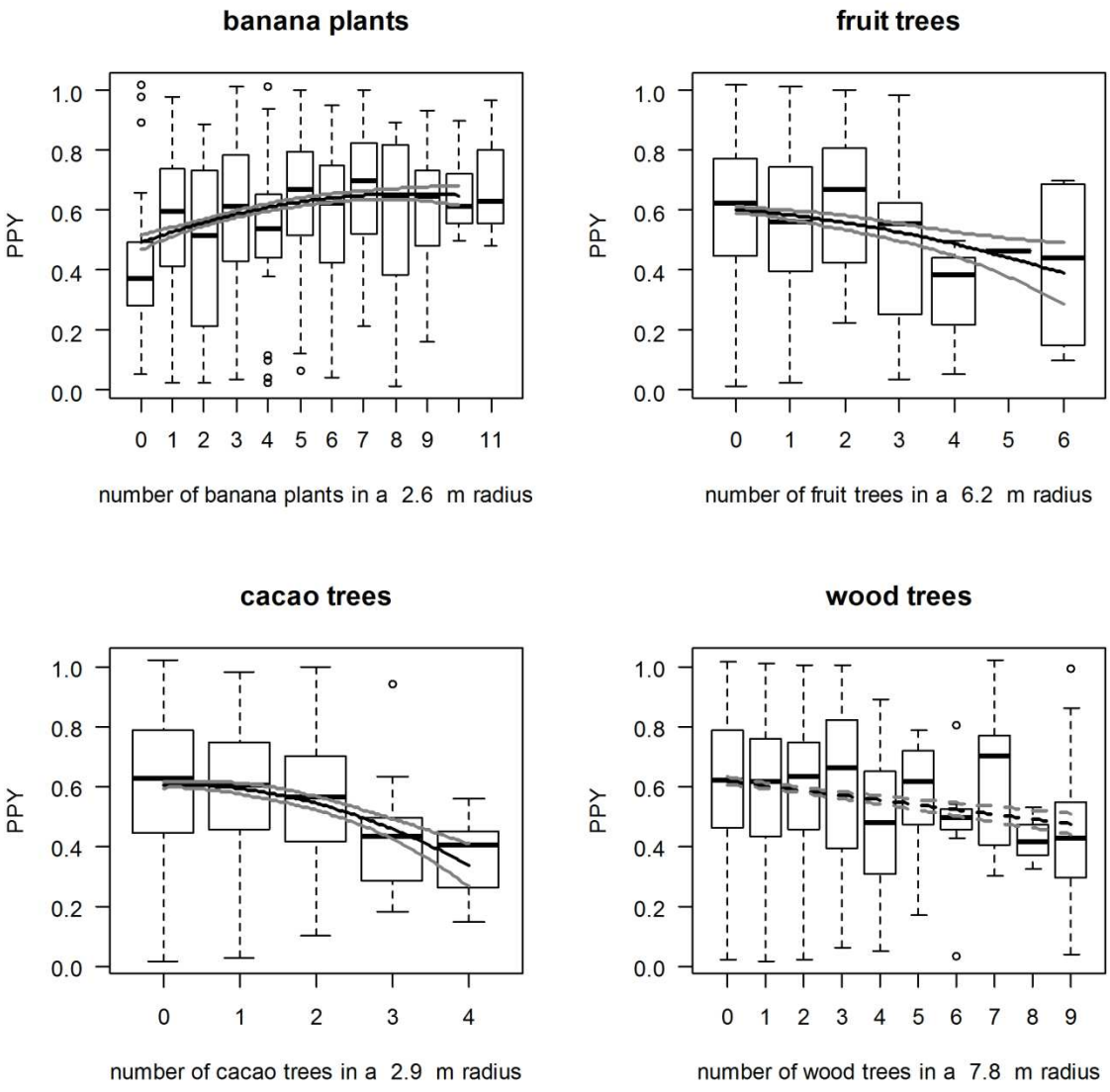

Figure 5. *Model fit of the predictions of the proportion of potential yield (PPY) of banana according to the number of banana plants in a 2.6 m radius, fruit trees in a 6.2 m radius, cacao trees in a 2.9 m radius, and wood trees in a 7.8 m radius. The black lines show the mean responses, and the grey lines show the standard errors predicted by the ´lmer´ (dashed-lines show non-significant relations).*

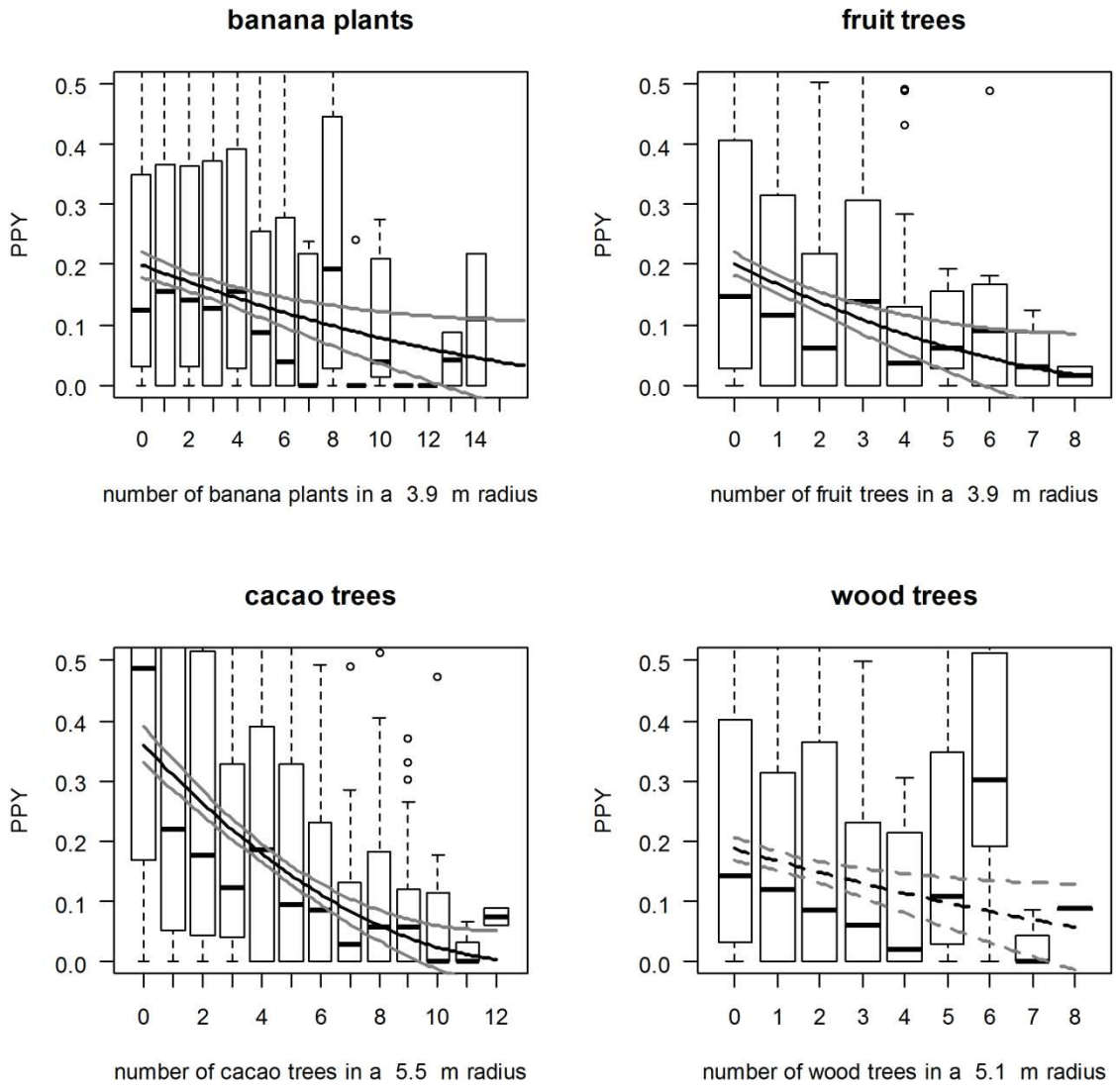

Figure 6. *Model fit of the predictions of the proportion of the cacao potential yield (PPY) according to the number of banana plants in a 3.9 m radius, fruit trees in a 3.9 m radius, cacao trees in a 5.5 m radius, and wood trees in a 5.1 m radius. The black lines show the mean responses, and the grey lines show the standard errors predicted by the ´lmer´ (dashed-lines show non-significant relations).*

4. Discussion

Overall, we found that the area around a banana or cacao plant (as indicated by a radius) that had the greatest effect on PPY was greater for larger neighbouring plants than for smaller neighbouring plants. In the banana PPY model, for example, the radius that had the largest effect on banana PPY was greater for the larger neighbors (fruit or wood trees) than for smaller neighbors (cacao trees or banana plants). The radii that had the greatest effect on PPY were smaller in the cacao PPY model than in the banana PPY model probably because cacao trees are larger than banana plants. We found that the number of banana plants in a radius of 2.6 m had a significant positive influence on banana PPY, while cacao trees in a 2.9 m radius and fruit trees in a 6.2 m radius had significance negative influence. We suggest that this surprising result may be attributed to crop management, which tends to be better when banana density is high rather than low (*unpublished observations*).

Wood trees in the neighborhood of banana plants and cacao trees tended to reduce the PPY but the effect was not statistically significant. Even though wood trees were more numerous than fruit trees in the neighborhood of banana plants and cacao trees, the effect of fruit trees was statistically significant but that of wood trees was not. This difference may be attributed to the position of the trees in the canopy and to the resulting effects on shade intensity (Gidoin et al. 2014), fruit trees also have denser canopies than wood trees (Somarriba et al. 2014). Because wood trees are high in the canopy (Ngo Bieng et al. 2013), they provide a low level of uniform shading to the shorter banana plants and cacao trees. This suggests that wood trees at an adequate density and spatial distribution should not affect banana and cacao productivity, which is important because wood trees help provide other ecosystem services in cropping systems (Tscharntke et al. 2011). Relative to wood trees, fruits trees provide more localized and more intensive shade (Gidoin et al. 2014). This more localized shade may reduce banana and cacao productivity. Ours results agree with previous studies that described a positive correlation between yields and light availability when growth is not limited by nutrient availability (Vernon 1967, Jucker et al. 2014). This suggests that when light becomes scarce, complementarity is reduced. The latter

hypothesis is consistent with findings of Zuidema et al. (2005), who showed that heavy shading (>60%) in agroforestry systems reduced yields by more than one-third.

Because our study was carried out on individual plants, it generated a large quantity of field data and was statistically powerful. Furthermore, the analysis of the most important distance (radius) for each type of neighboring plant without any *a priori* assumption provided new information on the distance at which plants interact. This assessment of distance also provides practical guidance for how neighboring plants may be organized to increase banana and cacao productivity. For example, our analysis (**Figure 4**) suggests that 4 banana plants in a 2.6-m radius, 2 cacaos trees in 2.9-m radius, 2 fruit trees in 6.2-m radius, and 2 wood trees in 7.8-m radius should not reduce banana productivity. These values correspond to densities per ha of 1884, 757, 166, and 105 for banana plants, cacao trees, fruit trees, and wood trees, respectively. In the case of cacao (**Figure 5**), 4 banana plants in a 3.9-m radius, 2 cacaos trees in 5.5-m radius, 2 fruit trees in 3.9-m radius, and 1 wood tree in 5.1-m radius should not reduce the cacao productivity. These values correspond to densities per ha of 838, 210, 421, and 122 banana plants, cacao trees, fruit trees, and wood trees, respectively.

For monocultures, the recommended densities are 1600–1900, 900–1100, 200–300, and 80-120 individuals ha^{-1} for banana plants, cacao trees, fruit trees, and wood trees, respectively (Robinson and Nel 1985, Wheaton et al. 1986, Wood and Lass 2008, Suatunce et al. 2009). These recommended densities in monoculture are similar to the optimal densities suggested by our models. For cacao, the average production measured in this study (191 Kg ha^{-1}) was low compared to the potential production (as high as 1800 Kg ha^{-1} in Malaysia, 800 Kg ha^{-1} in Ivory Coast, 350 Kg ha^{-1} in Ghana, and 250 Kg ha^{-1} in Central America) (Dormon et al. 2004). One likely reason for the low production of cacao trees in the current study was disease caused by the fungus *Moniliophthora roreri* and other pathogens (Leach et al. 2002).

In contrast to the production of cacao, the vegetative growth of bananas in the current study (which ranged from 9 and 11 Kg per banana plant in 17 weeks depending on the variety) is close to the potential of bananas as measured in intensively managed monoculture (Tixier et al. 2008, Ripoche et al. 2012). The

high productivity may be explained by the low levels of pests and diseases on bananas grown in agroforestry systems (Schroth et al. 2000, Staver et al. 2001). This suggests that the negative effects of neighboring trees on banana plants in our study resulted from competition for light and mineral resources. On an applied perspectives, it thus seems possible to grow highly productive banana plants in association with trees, especially with cacao trees and with moderate densities of bigger trees (about 100 fruit trees or 150 wood trees per ha). This result is consistent with Deheuvels et al., (2012), who showed that cacao yield per tree was significantly higher in combination with high than with low *Musa* densities, suggesting that the spatial distribution of plants may be more important than their botanical composition.

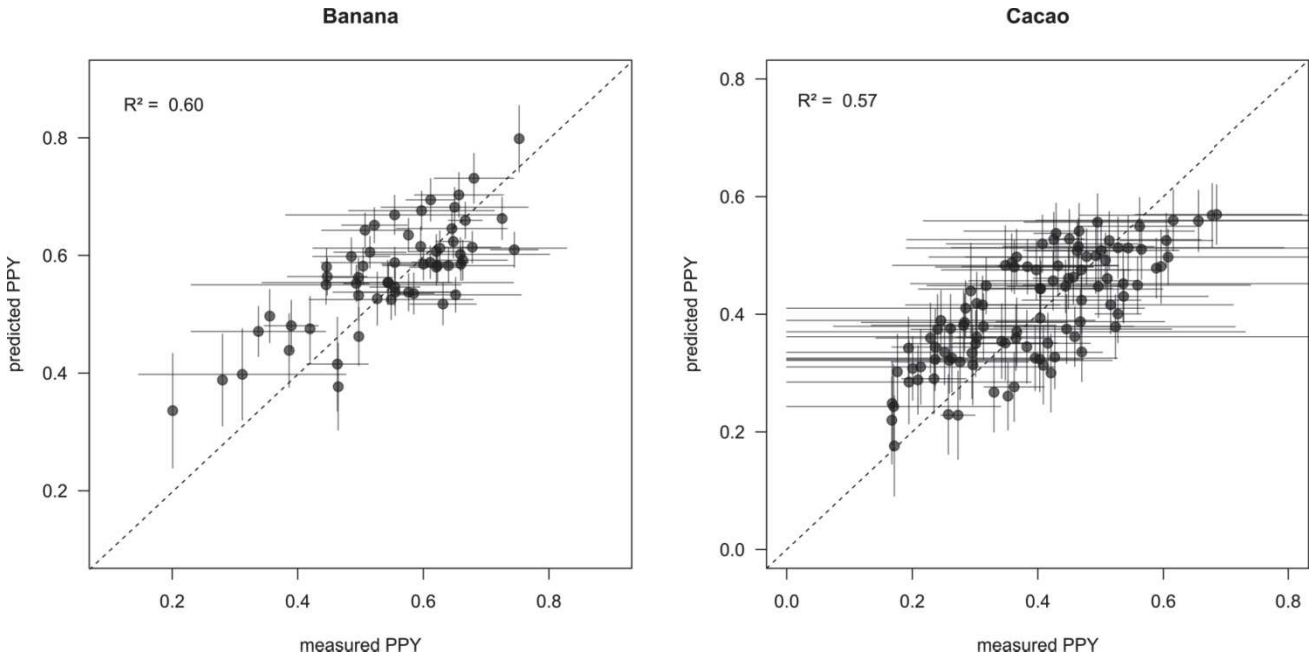

Figure 7. *Predicted vs. measured proportion of the potential yield (PPY) for banana plants and cacao trees for each existing assemblage of neighboring plants (i.e., number of banana plants, cacao trees, and fruits trees within the radius considered in the PPY models). Horizontal bars indicate the standard error, and vertical bars indicate the prediction error. The two models used for banana and cacao PPY predictions are presented in Table 1.*

Our statistical PPY models were relatively accurate in predicting the average effect of all plant assemblages (**Figure 7**); both models explained about 60% of the variance in PPY was explained, which could be considered as satisfying, especially when considering the low number of parameters used. It is not sure that process-based models can better explain the variance of plant productivity. However, it would certainly valuable to intend linking statistical models with more process-based models. The development of process-based models will certainly require a huge amount of measurements not only of plant growth (by organ) but also of environmental variables linked to the availability of resources (e.g., local soil nutrient content and radiation available for each plant). To our knowledge, sufficient measurements to build such process-based model have only been obtained in relatively homogeneous systems as coffee agroforestry systems (Roupsard et al. 2011, Charbonnier et al. 2013). Process-based models would be useful to better understand processes at play although there is a risk that they would be over-parameterized compared to statistical approaches as presented here.

5. Acknowledgments

We thank the farmers who allowed us to use their farms for this study. We also thank Alonso Porras, Bruno Lopez, Federico Gomez, and Marvin Lizano for assistance with data collection. This study, which received financial support from the Instituto Tecnológico de Costa Rica and Instituto Francés de América Central, is part of the Scientific Partnership Platform on Agroforestry Systems with Perennial Crop (PCP AFS-CP) led by CIRAD and CATIE. We also thanks Dr Raphaël Achard (CIRAD) for helping us to improve the allometric relation between biomass and circumference.

6. Supplementary Materials

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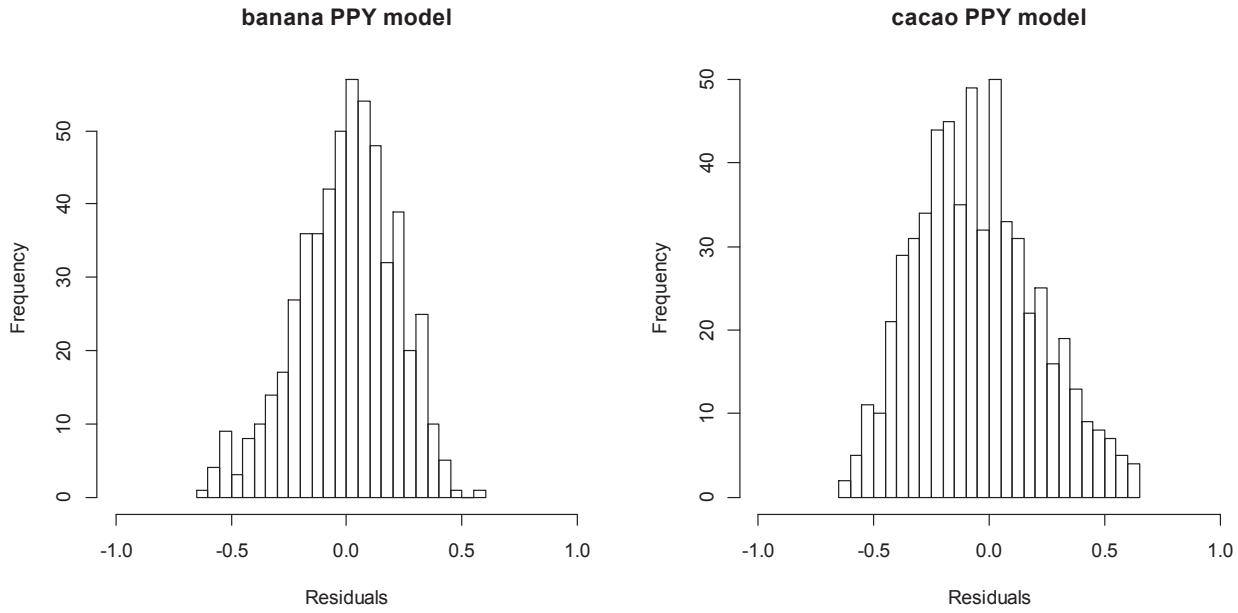

Figure S1. *Distribution of the residuals of the two complete models that predict the banana and cacao PPY based on the number of neighboring plant as presented in Table 1.*

Chapter 6 – General Discussion

In this section, I aimed at discussing globally the findings from the meta-analysis presented in Chapter 3 and the results from the analysis of the field study carried out in agroforestry systems of Talamanca presented in Chapter 4 and 5. My objective here is to synthesize the knowledge related to the plant richness/productivity hypothesis in order to draw directions to improve multi-species cropping systems.

1. The contribution of the study

1.1 Reconciling plant richness and productivity

Plant richness tends to have a positive effect on plant productivity in both natural and managed ecosystems (Barot et al. 2017). Although debates and controversies remain on the exact role of biodiversity in productivity (Loreau et al. 2001). Both ecology and agronomy can contribute to improvements of intercropping systems, even available evidence indicates that plant richness matters more in agricultural ecosystems than in natural ecosystems (Barot et al. 2017). In line with our meta-analysis, previous studies confirmed that annual intercropping and grassland mixtures experiments are likely to be more productive than monocropping (Li et al. 2014, Craven et al. 2016). The originality of our meta-analysis lies in the fact that we included a wide range of agroecosystems. We found that plant richness increases the overall ecosystem productivity but that the magnitude of this positive effect tends to decrease with the plant richness. In other words, the results suggest that the gain in productivity per unit of diversity added decreases as diversity increases. It suggests that if the objective is solely the productivity, highest yield may be obtained with moderate plant richness. Our meta-analysis also showed, that the responses of productivity to plant richness were smaller for agroforestry systems than for annual plants systems (estimated though the effect size) (see **figure 2F, Chapter 3, p55**). This

suggests that the issue of light partitioning is probably a strong factor that may be taken in consideration when designing “biodiversified” schemes.

Our study of multispecies agroforestry fields in Talamanca confirmed these findings for the main cash crops (banana and cacao). Although the global income per plant was positively correlated with plant diversity, the values of banana and cacao were clearly negatively correlated with plant diversity. The positive relationship between global incomes and plant diversity was largely explained by income generated by higher strata plant groups (wood and fruit trees). We can hypothesize that there was no (or few) complementarity between lower and higher strata plants. The asymmetry in accessing light probably explains the inverse production/diversity relation observed between strata. Our meta-analysis suggests that plant diversification is more likely to increase production when it occurs in a single stratum. However in our measures in agroforestry systems, the negative correlation between income from low strata plants and plant richness is rather weak (**Figure 1**), this finding could also depends on the shading tolerance of species.

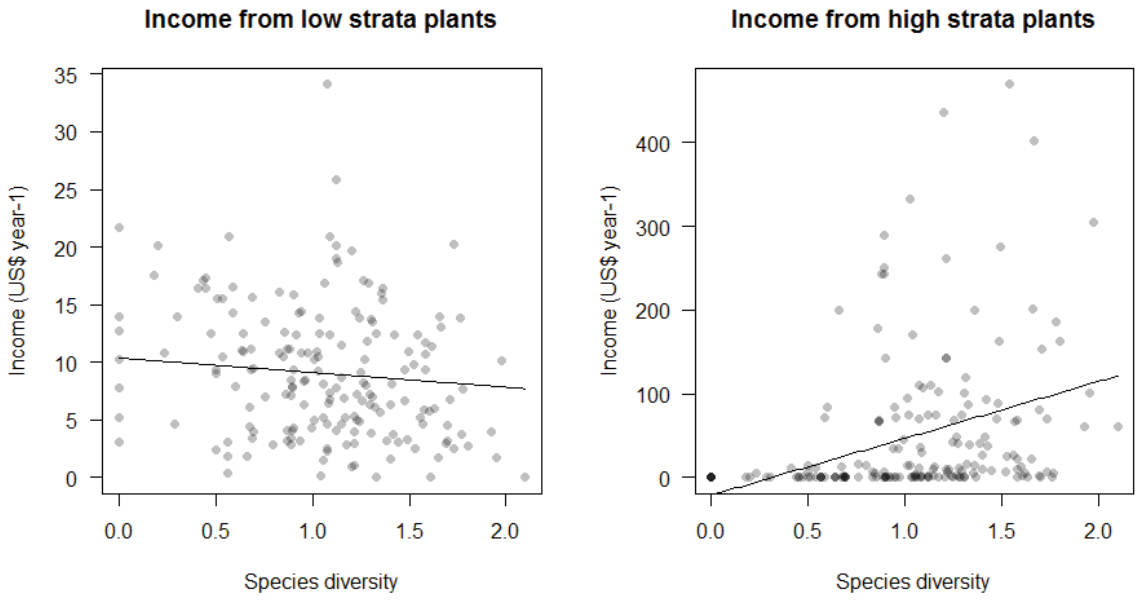

Figure 1. *Total mean income (global income) for higher strata plant groups (timber wood and other fruit trees) and lower strata plant groups (banana and cacao) in response to plant species diversity in 20 agroforestry fields in Talamanca, Costa Rica. Diversity was assessed using the Shannon–Wiener index. Each circle indicates the mean value from one of the 180 plots. The lines*

show the prediction of the generalized linear model that included field as a random effect.

1.2 Application of the statistical modelling to complex agroforestry systems

Methods for technology development in complexity multispecies systems barely exist. In particular, the modelling tools widely used in agronomy are not well adapted to assess and design sustainable multispecies cropping systems (Malézieux et al. 2009). In our meta-analysis the complete statistical model suggests that perennial plants may help stabilize the productivity across a broad range of plant richness, a general idea that is in line with agroecology. To tackle the very high level of complexity of agroforestry fields in Talamanca, we developed a statistical approach based on the response of individual plants to their neighbours. The originality of this method lies in:

i) The individual analysis. This was particularly crucial because in such diversified systems, the spatial structure may display a high variability that makes the neighborhood of each plant different.

ii) The use of a method similar to yield gap analysis to determine the potential growth of banana and cacao according to their initial size (called percentage of the potential yield PPY). This approach allowed us to take into account the fact that the growth or the yield of a given plant is not only depending on its environment but also to its size. Through this approach, it was possible to take into account the fact that the vegetative growth of banana stop after flowering and that young and old cacao trees produce less pods than mid-age ones.

iii) The fact that we did not choose an *a priori* distance of effect between plants. Knowing at what distance plants are likely to interact is useful 1) to build a model and 2) to provide practical guidance on how plants may be organized in the fields to increase banana and cacao productivity.

Our study generated a large quantity of field data from individual plants that allow us to analyze the productivity according to the specification of the four categories of plants groups assigned: i) banana, ii) cacao, iii) wood trees, and iv) fruits trees, we defined this approximation because it is closer to the reality of farmers in terms of commercial products. However, it may have some limits to deal with functional groups rather that with species or varieties of plants, for instance in a same group, some species could be more productive than others.

1.3 Competition versus complementarity

Multispecies systems may maximize beneficial interactions while minimizing competition for space, competition for light between canopies, and competition for water and nutrients between root systems. The ecologist provides a rich theoretical framework for approaching the role of biodiversity in productivity. However in cultivated ecosystems there is few application for this theoretical framework (Malézieux et al. 2009). Mixed plants species in cropping systems requires a carefully analysis, because of triggered complementarity effect hypothesis (Barot et al. 2017).

In our meta-analysis, we found that the response of productivity to plant richness was affected by the type of plants (annual or perennial) in the community and the strata level layers of the canopy structure (multi-strata, mono-strata). The effect of plant richness on the productivity, for example, was reduced by the presence of trees in the canopy (see **figure 2E, Chapter 3, p55**). These findings are in line with the results of our models of agroforestry systems in Talamanca. We suggest that the negative relationship between income generated by lower strata plant group (banana and cacao) and the positive relationship between income generated by higher strata plant group (wood trees and other fruit trees) with plant diversity, are resulted from belowground and aboveground competition, but mainly we suspect that trees, by greatly reducing the solar radiation for the lower strata plant group. Similar results have been reported in tropical and temperate forests (Hooper et al. 2005, Zhang et al. 2012, Jucker et al. 2014).

Competition rather than complementarity apparently dominated for the lower strata cultivated plants. When light becomes scarce, complementarity is reduced (Reich et al. 2003, Dybzinski et al. 2008, Lebauer and Treseder 2008, Jarchow and Liebman 2012). Barot et al. (2017) also add that possible high variances in architectural traits could also impact the microclimate in and below the canopy structure and modify productivity.

The capture and use of solar radiation received an important attention in multi-species systems, overyielding by mixtures have often been attributed to more efficient use of light by their canopies. (Keating and Carberry 1993, Malézieux et al. 2009). We suspect that the availability of solar radiation, which decreases with latitude (Budyko 1969), might alter the relationship between plant richness and productivity. The strong solar radiation at lower latitudes might promote complementarity between plant species, while the weaker radiation at higher latitudes might promote competition and thereby dampen the effect of plant richness (see **figure 6B, Chapter 3, p64**). We confirm that the design of plant-diversified systems should take into account the local availability of solar radiation as determinant environmental factor.

Our findings also triggers paradigmatic–stress gradient hypothesis which predicts a linear increase in the intensity of facilitation (that is a type of complementarity) as environmental conditions become increasingly stressful (Bakker et al. 2013). Our results are consistent with the resource availability—competition intensity hypothesis, which predicts that competition increases with productivity of the species involved and on the nature of the stress (Maestre et al. 2009). However, the slower decrease of the effect size in the case of systems that includes perennials compared to those with only annuals (see **figure 6A, Chapter 3, p64**), suggests that for systems that are prone to strong variation (environmental, compositional and temporal) the addition of trees may be an option to stabilize yield.

1.4 Implication of results for the management of AFS

As mentioned before, previous meta-analyses showed how mixtures of plants could be beneficial to the yield; However, it should be addressed that these

studies focused either on short-term experiments with annual (Yu et al. 2015) either on grasslands without an upper canopy layer (Cardinale et al. 2007, Li et al. 2014, Craven et al. 2016). Our results failed to show that the stratification of canopy layers promotes complementary effects in resources exploitation (Parker 1995, Fridley 2003). However, our analysis predicted that the variability in effect size for systems increases with the level of the plant richness in systems with only annuals but is stable in systems with perennials. This suggests that perennial plants may help stabilize the productivity across a broad range of plant richness. In future meta-analyses and field studies, it would be valuable to further evaluate the relationship between productivity stabilization and plant richness.

From an agroforestry perspective, our results suggest that the intercropping with plants that occupy different canopy strata does not lead to overyielding. This is especially likely to be the case for high productivity systems, in which light is often a limiting factor and in which tall plants out compete shorter ones (Rajaniemi 2003). In such systems, different species are more likely to compete for light than participate in light partitioning. More research is needed to better understand light partitioning between crops because light partitioning is often considered in the design of intercropping systems (Allen et al. 1976, Ewel 1986, Cruz and Sinoquet 1994).

Overall, we found that the number of plants inside an area around a banana or cacao plant (as indicated by a radius) had a greater negative effect on PPY for larger neighbouring plants (fruit or wood trees) than for smaller neighbouring plants (cacao trees or banana plants). In the banana PPY model, the radius that had the largest effect on banana PPY was greater for the larger neighbors than for smaller neighbors (see **figure 5 Chapter 5, p99**). We found that the number of banana plants in a radius of 2.6 m had a significant positive influence on banana PPY, while cacao trees in a 2.9 m radius and fruit trees in a 6.2 m radius had significance negative influence. We suggest that this surprising result may be attributed to crop management, which tends to be better when banana density is high rather than low (*unpublished observations*).

1.4.1 Application to the Talamanca case

The 180 agroforestry plots on the 20 fields in Talamanca, Costa Rica, exhibited a large range of plant diversity (the Shannon–Wiener index ranged from 0 to > 2, with a total of 56 species of cultivated plants). The high range in species diversity observed in this study was similar to that observed in previous studies (Borge and Castillo 1997, Guiracocha 2000, Anglaaere et al. 2011, Deheuvels et al. 2012, Ngo Bieng et al. 2013). Plant density and spatial organization suggested that farmers consider banana and cacao as the primary crops and timber and other fruits as secondary or complementary crops.

As pointed out by the farmers interviewed, these complex cultivated plant communities, reflect two main management strategies: i) to establish cacao and banana in remnant forests and ii) to establish other fruits during the natural regeneration of timber and firewood trees. Trees from natural regeneration are usually preferred because they do not have to purchase plantlets. In addition, regenerated trees are generally thought to be better adapted than planted trees to site conditions (de Sousa et al. 2016).

Banana was the most abundant group with an average population density of 1100 plants ha1, which is not very different from the population density in intensively managed commercial plantations (1600 to 1900 plants ha-1). This highlights the importance of banana to the agroforestry farmers in Talamanca.

Recommended densities in monoculture are similar to the optimal densities suggested by our models. However for cacao, the average production measured in this study (191 Kg.ha-1) was low compared to the potential production (1800 Kg.ha-1 in Malaysia, 800 Kg.ha-1 in Ivory Coast, 350 Kg.ha-1 in Ghana, and 250 Kg.ha-1 in Central America) (Dormon et al. 2004). In contrast to the production of cacao, the vegetative growth of bananas in the current study (which ranged from 9 and 11 Kg per banana plant in 17 weeks depending on the variety) is close to the potential of bananas as measured in intensively managed monoculture (Tixier et al. 2008, Ripoche et al. 2012). This result is consistent with Deheuvels et al., (2012) , who showed that cacao yield per tree was significantly higher in combination with high than with low Musa densities, suggesting that the spatial distribution of plants may be more important than their botanical composition.

This finding also suggest that low strata crops (banana and cacao) could be more productive when there are less competing of high strata crops (fruits and wood trees)

The average productivity of cacao was 191 Kg.ha-1 year-1, which was somewhat higher than the 136 Kg.ha-1 year-1 reported by Deheuvels et al. (2012) for similar agroforestry systems in Talamanca. Such yields are substantially lower than those of cacao agroforestry systems in Ghana and Ivory Coast, which average 456 and 214 Kg.ha-1.year-1, respectively (Gockowski and Sonwa 2011). As noted by Deheuvels et al. (2012) and Leach et al. (2002), the lower cacao yields in Talamanca result from the absence of chemical input and from losses caused by the fungus Moniliophtora roreri, the agent of cacao frosty pod rot disease.

The average Cordia alliadora timber production in the current study (26 m3.ha-1) was substantially lower than the 48 m3.ha-1 recently reported for Central America (Somarriba et al. 2014). This may result from differences in sites and planting densities. Although the yields in the current study are low, they clearly represent a key economical input for smallholders, especially when cacao prices are low (Ramírez et al. 2001). Compared to timber, firewood is not a key economic input and averaged 43 trees per ha, which corresponds to 5.25 m3.ha-1. According to the farmers interviewed, these species are not sold but are used by the farmers themselves.

The evaluation of the productivity of other fruits trees was difficult because of their seasonal variation. Our estimation of income from these fruits tree is clearly higher than other cultivated plants (see **figure 2, Chapter 4, p77**). Although farmers have no production records, this result is consistent with farmer's perception since they claim good yielding for fruit trees.

Even though wood trees were more numerous than fruit trees in the neighborhood of banana plants and cacao trees, the effect of fruit trees on productivity was statistically significant while the effect of wood trees was not. This difference may be attributed to the position of the trees in the canopy and to their effects on shade intensity (Gidoin et al. 2014). Because wood trees are high in the canopy (Ngo Bieng et al. 2013), they provide a low level of uniform shading to the shorter banana plants and cacao trees. This suggests that wood trees at

an adequate density and spatial distribution should not strongly affect banana and cacao productivity. This result is very important because maintaining high trees in the system helps providing other ecosystem services in cropping systems (Tscharntke et al. 2011). Compared to wood trees, fruits trees provide more localized and more intense shade (Gidoin et al. 2014). This more localized shade was showed to reduce significantly banana and cacao productivity. Ours results agree with previous studies that described a positive correlation between yields and light availability when growth is not limited by nutrient availability (Vernon 1967, Jucker et al. 2014). The latter hypothesis is consistent with findings of Zuidema et al. (2005), who showed that heavy shading (>60%) in agroforestry systems reduced yields by more than one-third.

By opposition to the production of cacao, the high productivity of bananas may be explained by the low levels of pests and diseases on bananas grown in agroforestry systems (Schroth et al. 2000, Staver et al. 2001). On an applied perspectives, it seems possible to grow highly productive banana plants in association with trees, especially with cacao trees and with moderate densities of bigger trees (about 100 fruit trees or 150 wood trees per ha).

This could lead to some specialization within fields such that banana is grown in one part of the field and other trees are grown in other parts (**Figure 2**).

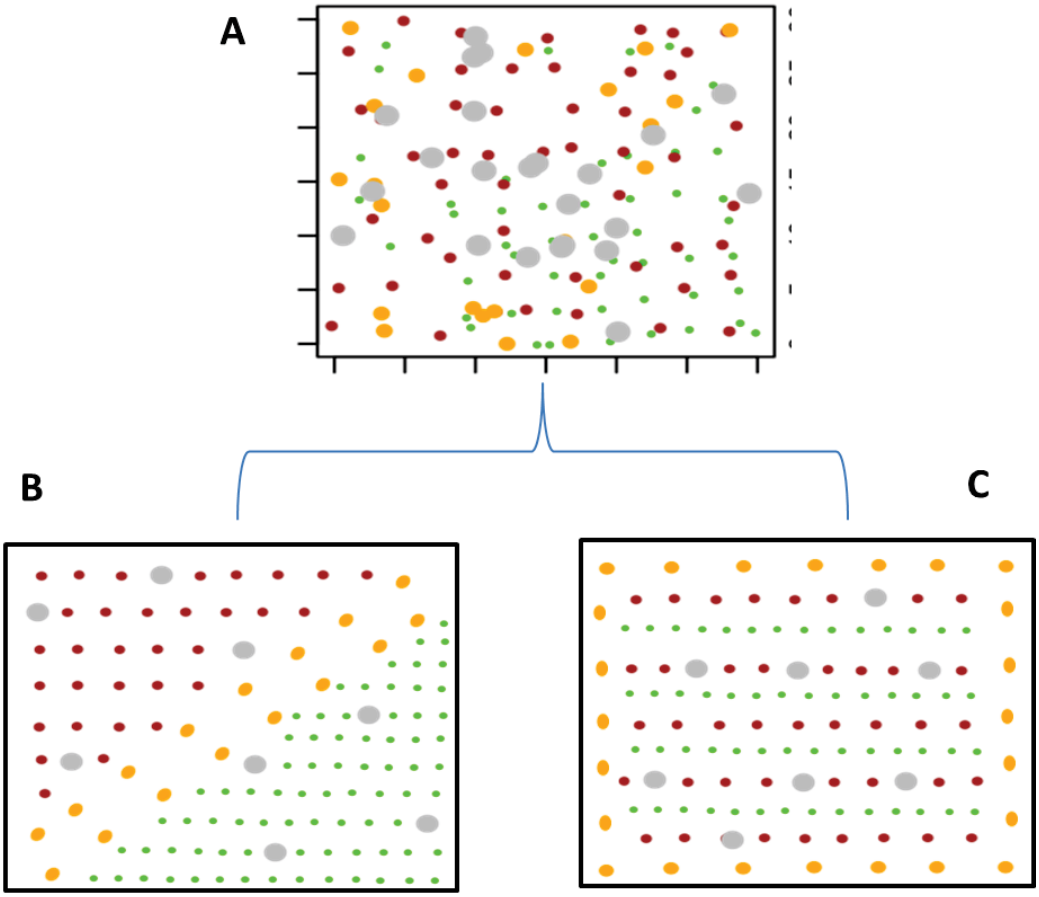

Figure 2. *Possible evolutions of the organization of agroforestry fields. Each point represents a plant from one of the four categories (green: banana plants, brown: cacao trees, orange: fruit trees, grey: wood trees). "A" represents an example of the current spatial distribution in agroforestry systems (field 5). "B" and "C" represent two possible spatial organizations that should make possible growing highly productive banana plants and cacao trees in association with high strata trees.*

2 Perspectives

2.1 Reflections on the approach of future studies

Main (1999) suggest that there is no absolute answer to the question of how much biodiversity is enough because all systems are dynamic. Our methodology approach and the field protocol confirmed this, suggested that the effect of plant diversity on the performance of agroforestry systems is a tight balance between objectives of farmers and the manageability that they assumed in the design of multispecies cropping systems. The originality of this thesis was to adapted methods to develop some approaches to access the relationship between diversity and productivity. My recommendation for future works is to develop models that combine statistical approaches and process-based methods that will require more measurements not only of plant growth (by organ) but also of environmental variables linked to the availability of resources (e.g., local soil nutrient content and radiation available for each plant). Obtaining such measurements for individual plants is difficult in highly diversified and complex systems. To our knowledge, sufficient measurements to build such process-based model have only been obtained in relatively homogeneous systems as coffee agroforestry systems (Roupsard et al. 2011, Charbonnier et al. 2013). This approach will help us to simplify the effect of crops on local resources, while maintaining a mechanistic approach to crop yield, disease regulation and pollination services, to determine whether they can attain high levels of productivity.

This thesis could feed the framework proposed by Cardinal et al. (2012a) that links biodiversity to the goods and services provided by ecosystems, mainly in productivity or yield terms. Future studies and meta-analyses should determine how plant diversity affects the ability of systems to provide multiple ecosystem services and not simply productivity or yield.

2.2 Reflections on modelling approaches

Multispecies systems are today a real challenge for systemic agronomy research. Modelling research on multispecies systems still remain reduced, although many

models have been developed to simulate the growth and activity of weed, pest and diseases populations (Malézieux et al. 2009). Integration of scientific and empirical knowledge is particularly needed to represent interaction between management practices, biodiversity, and ecosystems services. Model-based processes approaches seem a promising way to support stakeholders involved in a biodiversity-based agricultural process. This raises question about how to build for a wide diversity agricultural context, the appropriate level for analytical and modelling methods of agroecological practices required to deliver expected ecosystems services (Duru et al. 2015).

The present thesis used individual based statistical models to analyze the interactions between plants among the community of agroforestry systems. The results of this research provide new information on the effect of spatial organization on productivity and contribute to propose new organizations for these agroforestry systems. Future studies may try to tackle how such statistical models may be linked or used jointly with processes based models. For example, it could include processes that link pest and disease damages on the plant growth or an explicit partitioning of resources (nutrients and light).

3 General conclusion

As pointed by Malézieux et al. (2009), even when advantages are recognized, multispecies systems are sometimes more difficult to manage and require substantial farmers skills and specific research effort to develop knowledge on more biological models. In particular for complex agroforestry studies is more complicated to define a proper methodology compared with studies involving simple multispecies systems, because is due to the specificity of their vertical and horizontal organization that is particularly diverse. More generally, the interpretation of mechanisms influencing biodiversity-productivity relationship and resources in the environment is extremely complex. It remains very difficult to disentangle those processes experimentally. From a methodological point of view the specificity of my thesis is that the statistical approach was carried out at

the individual plant scale. At this scale, it was possible to take into account the particular neighborhood of each plant. My meta-analysis suggests that perennial plants may stabilize productivity, the individual-based analysis suggest that for moderate densities of trees do not decrease dramatically the cash crops yield. Put together, this knowledge suggests that we can optimize and stabilize the productivity by keeping adequate densities of trees in the system. The results of this research provide new information that allow better understanding these agroforestry systems and that would be helpful to establish recommendations to farmers on how to increase productivity.

These results emphasize that future studies on the effects of species richness on productivity should include a wide range of biotic and environmental factors, and a large strata level gradients in the above-ground vegetation. This would make easier identifying conditions under which species richness is most likely to have a positive effect on productivity. We confirm that the design of plant-diversified systems should take into account the local availability or resources.

Our analysis of productivity of banana and cacao suggests that complementarity might be increased by increasing plant diversity within the same stratum of the canopy or with moderate abundance of very high stratum. In the case of fruit trees, our results suggest that the planting densities should be choose according to a trade-off: a small to moderate increase in the density of fruit trees may significantly increase farmer income, but when densities of fruit trees are too high the shading effect implies production loss on the main cash crops (cacao and banana). However fruit trees production is limited by a poor access to markets in the region. It would be easier to farmers to improve their livelihood by valuing fruit tree production than to improve management practices related to specialization of their farms by decreasing plant diversity. Extension services and government incentives should probably focus on organizing distribution channels to facilitate the sale of fruits from these systems.

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Annexes

A. Annexes - Soil sampling

Initially the objective was to use the information of soils for the analysis in this thesis, but the results were not conclusive, so this information is given here as descriptors of the studied agrosystems. The description of the analysis of the soil samples of the 20 plots was relatively constant between them. 27 soil samples were taken per plot, collected at a depth of 30 cm. Once the 27 samples were obtained they were well mixed in a clean bucket until having a sample as composed as possible. The 20 total samples were sent to the University of Costa Rica, Agronomic Research Center (CIA) for the soil analysis. A chemical KCl-OLSEN (pH, acidity, Ca, Mg, K, P, Cu, Fe, Zn, Mn), organic matter and total N was analyzed.

Table 1. Total soil chemical analysis of the 20 plots in study.

Extract Solution:	pH	cmol(+)/L					%	mg/L				
KCl-Olsen	**H_2O**	**ACIDITY**	**Ca**	**Mg**	**K**	**CICE**	**SA**	**P**	**Zn**	**Cu**	**Fe**	**Mn**
ID Farmer	**5,5**	**0,5**	**4**	**1**	**0,2**	**5**		**10**	**3**	**1**	**10**	**5**
RICARDO	6,2	0,16	11,26	2,10	0,19	13,71	1	7	1,0	6	144	14
LAYAN	5,3	0,69	15,20	9,02	0,13	25,04	3	1	4,5	10	91	61
ALONSO	6,6	0,13	10,58	1,60	0,23	12,54	1	7	0,9	5	91	12
AMADEO	4,9	5,42	6,91	3,89	0,28	16,50	33	2	3,5	8	177	102
RUTH	5,4	0,82	24,41	10,08	0,20	35,51	2	1	4,4	9	58	75
ISMAEL	5,9	0,23	18,82	4,93	0,25	24,23	0,9	4	1,3	6	89	15
ANA	5,0	1,89	4,13	1,52	0,15	7,69	25	2	1,9	6	218	41
TONY	5,0	3,16	10,24	7,51	0,15	21,06	15	3	4,7	9	173	100
MARIA	6,3	0,18	11,34	2,43	0,17	14,12	1	9	1,2	7	161	34
ELSA	6,2	0,18	30,90	6,93	0,51	38,52	0,5	7	2,7	18	56	13
CARMEN	5,0	2,79	6,46	3,58	0,14	12,97	22	1	3,8	4	167	123
ASDRUBAL	6,6	0,13	30,56	5,15	0,31	36,15	0,4	4	2,9	7	55	8
DARIA	5,4	0,77	6,57	1,85	0,11	9,30	8	7	0,7	7	227	10
ANABELLE	5,6	0,59	6,72	1,66	0,13	9,10	7	9	0,7	8	180	11
WILFREDO	5,8	0,25	24,65	6,31	0,36	31,57	0,8	2	5,5	5	95	23
ROSEMARY	5,7	0,33	8,88	2,17	0,20	11,58	3	12	0,9	11	236	13
ELISEO	6,1	0,15	8,15	2,28	0,24	10,82	1	9	0,9	9	152	12
JOSE MARIA	6,1	0,17	7,64	1,56	0,15	9,52	2	4	0,7	8	127	9
SARA	5,6	0,26	24,21	6,68	0,42	31,57	0,8	1	4,8	6	74	56
MARINA	5,5	0,23	19,43	5,51	0,44	25,61	0,9	4	7,3	5	82	38

The values below each element correspond to the General Critical Levels for the used extract solution

CICE = Cation exchange capacity Effective = Acidity + Ca + Mg + K

SA = Percentage of Acidity Saturation = (Acidity / CICE) * 100

Table 2. Organic matter and total nitrogen soil chemical analysis of the 20 plots in study.

	mS/cm	Relation		
ID Farmer	**CE**	**C**	**N**	**C/N**
RICARDO	0,1	1,45	0,13	11,2
LAYAN	0,1	1,71	0,20	8,6
ALONSO	0,1	0,92	0,08	11,5
AMADEO	0,1	1,58	0,19	8,3
RUTH	0,1	2,19	0,24	9,1
ISMAEL	0,1	1,26	0,15	8,4
ANA	0,1	1,40	0,15	9,3
TONY	0,1	2,25	0,26	8,7
MARIA	0,1	0,90	0,10	9,0
ELSA	0,1	1,13	0,14	8,1
CARMEN	0,1	1,18	0,17	6,9
ASDRUBAL	0,1	1,08	0,15	7,2
DARIA	0,1	1,37	0,17	8,1
ANABELLE	0,1	1,29	0,17	7,6
WILFREDO	0,1	1,49	0,20	7,4
ROSEMARY	0,1	1,58	0,19	8,3
ELISEO	0,1	0,96	0,12	8,0
JOSE				
MARIA	0,1	0,95	0,12	7,9
SARA	0,2	1,89	0,30	6,3
MARINA	0,1	1,75	0,21	8,3

Abstract

Adding plant diversity is increasingly presented as a mean to improve the sustainability of agrosystems. However, there is still a lack of knowledge on how plant functional diversity alters processes that support production. Because they cover a broad range of plant diversity, agroforestry systems in the tropics are a good case study to better understand the diversity-production relation. Agroforestry systems in the Talamanca region in Costa Rica are particularly interesting because among the cultivated plants they encompass, banana and cacao are two cash crops of major importance and for which production can easily be quantified and analyzed. Another specificity of these systems is that their vertical and horizontal organization is particularly diverse. Understanding how plant diversity and its organization alter the performances of these complex systems is particularly challenging and requires developing new approaches. The objectives of this thesis were to address the following questions: i) Which factors affect the relationship between plant diversity and productivity? ii) How plant diversity influences the global productivity of agroforestry systems? and iii) How the spatial structure of the plant community affects yields?

First, a meta-analysis was carried out to address the diversity-production issue among a very broad range of systems world-wide. This analysis focused on how latitude, climate, and canopy structure modify the effect of plant richness on productivity of agricultural and natural ecosystems. It showed that the gain per unit of diversity added decreased as plant richness increased. Our findings also showed that the response of productivity to plant richness largely depends on the type of plants in the community, especially if the community includes trees.

Then, we extensively studied the diversity and the productivity of 180 plots (100 m² each) located within 20 fields in the Talamanca region. A global evaluation of the productivity of these systems was possible with the estimation of the production of each plant during 1 year. This production was converted into income according to local market prices. While we observed a global positive effect of plant diversity on global income, this effect was contrasted according to the functional group considered (banana, cacao, other fruits, timber, and firewood). When considering the functional group separately, there was a positive effect of plant diversity for higher strata groups (other fruits, firewood, and timber) and a negative effect for lower strata groups (banana and cacao). This suggested that complementarity between plants was stronger than competition for those plants occupying the higher strata of the canopy but that competition was stronger than complementarity for plants occupying the lower strata of the canopy.

The second part of the analysis of the Talamanca fields dataset focused on the effect of neighbouring plants on the production of banana and cacao plants. An individual-based analysis was developed to determine whether the number of neighbouring plants of a given functional groups explained the potential yield of each banana or cacao plant. We found that the distance at which other plants alters the yield of banana or cacao plants was greater for larger functional groups (fruit or wood trees) than for smaller ones (cacao trees or banana plants). Interestingly, higher strata trees had a smaller effect than lower strata trees, suggesting that moderate densities of tall trees could be compatible with high banana and cacao production. These findings were discussed in terms of complementary and competition with respect to the availability of light at higher and lower strata of the canopy. On an applied perspective, our results suggest that productivity could be maximized by a reasonably number of plant species, and then we proposed new direction to organize fields in order to maximize the production of cash crops while providing supplementary income for farmers and ecosystem services.

Keywords
Multistrata agroforestry systems, Productivity, Plant richness, Biodiversity, Potential yield, Spatial organization, Costa Rica.

Résumé

L'ajout de diversité végétale est présenté comme un moyen d'améliorer la durabilité des agrosystèmes. Cependant, il y a encore des manques importants de connaissances sur l'effet de la diversité végétale sur les processus à la base de l'élaboration des rendements. Les systèmes agroforestiers tropicaux couvrent une large gamme de diversité végétale ; ce sont donc de bons modèles pour étudier la relation entre diversité et productivité. Les systèmes agroforestiers de la région de Talamanca au Costa Rica sont particulièrement intéressants car au sein de communautés végétales complexes. Ils comprennent des bananiers et des cacaoyers qui sont des cultures de rente importantes et dont la production peut facilement être quantifiée et analysée. Une autre spécificité de ces systèmes est qu'ils présentent des organisations spatiales particulièrement diverses. Analyser comment la diversité des plantes et son organisation influencent les performances de ces systèmes est particulièrement complexe et nécessite le développement de nouvelles approches. Les objectifs de cette thèse étaient d'étudier : i) quels facteurs affectent la relation entre diversité végétale et productivité ? ii) Comment la diversité végétale influence la productivité globale des systèmes agroforestiers ? et iii) Comment la structure spatiale des communautés de plantes cultivées influence leurs rendements ?

Tout d'abord une méta-analyse a été menée afin d'étudier la relation entre diversité végétale et production dans une très large gamme de systèmes naturels et cultivés. Cette analyse a notamment traité du rôle de la latitude, du climat et de la structure de la canopée sur cette relation. Elle a montré que le gain lié à la diversité végétale tend à diminuer avec la magnitude de cette diversité. Nos résultats montrent également que la réponse de la productivité à la richesse spécifique en plantes dépend énormément du type de communauté considéré, notamment si la communauté comprend des arbres.

Ensuite un réseau de 180 placettes situées dans 20 parcelles d'agriculteurs a été étudié dans la région de Talamanca. Pendant un an, la production de chaque plante a été évaluée. Cette production a ensuite été convertie en revenus en accord avec les prix du marché local. Alors qu'un effet positif de la diversité végétale cultivée a été observé sur le revenu globale (de chaque placette), cet effet était très contrasté si on le considérait séparément pour les différents groupes fonctionnels. Cet effet était positif pour les plantes des groupes appartenant aux strates hautes et négatif pour les plantes des groupes appartenant aux strates basses. Ces résultats suggèrent que la complémentarité entre plantes était plus forte pour les plantes des strates hautes et qu'inversement la compétition était plus forte dans les strates plus basses.

La seconde phase de l'analyse des données de ce réseau de parcelles a visé à étudier l'effet du voisinage de chaque bananier ou cacaoyer sur leur production. Une approche d'analyse individu-centrée a été développée afin de déterminer si le nombre de voisins d'un groupe donné dans un rayon donné était un bon prédicteur de la croissance ou du rendement de chaque bananier ou cacaoyer. Les résultats montrent que la distance à laquelle la production d'un bananier ou d'un cacaoyer est affectée par ses voisins dépend de leur taille. De manière surprenante, les grands arbres ont eu un effet plus faible que les arbres plus petits. Cela suggère que des densités modérées de grands arbres pourraient être compatibles avec une production de bananiers et de cacaoyer avec un haut niveau de rendement. Ces résultats ont été discutés en termes de complémentarité et de compétition pour la lumière. Des pistes d'organisation sont proposées et discutées au regard de la maximisation des rendements des cultures de rente et des autres cultures mais aussi pour la provision de services écosystémiques au sens large.

Mots-clés
Systèmes agroforestiers multistrates, Productivité, Richesse spécifique, Biodiversité végétale, Rendement potentiel, Organisation spatiale, Costa Rica.